

FRUIT FALL PATTERNS IN AN EXPERIMENTALLY BURNED AMAZONIAN FOREST

By

ERIC OLIVEIRA CARVALHO

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2011

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To Antônio Galdino Oliveira and Noan Maia Carvalho

ACKNOWLEDGMENTS

I would like to thank first and foremost my parents Cecilia and Wilton Carvalho, for their unyielding and unconditional support and love through all my endeavors. Thanks to my siblings, Alex and Livia, for their love, friendship, and support they give their older brother. I thank Noan Carvalho who has given me inspiration, friendship, and love, always keeping me on my toes, and pushing me to become a better human being.

I thank Paulo Brando, without whom this thesis would not have been possible. Thanks to Leda Kobziar, my advisor, for giving me the opportunities to pursue research on themes that I believed relevant to my interests. I thank Jack Putz, for crucial mentoring and numerous insightful suggestions that made it possible to push this work forward. Thanks to Christie Staudhammer for her advice on various statistical analyses in this project.

Many thanks to the IPAM field crew of the Tanguru Ranch whose hard work makes possible works such as the present thesis.

Thanks to Morena Maia for sharing with me some of the most special moments in my life and for invariably making life a difficult challenge.

I thank Leonardo Pacheco, Pedro Constantino, Ana Carolina Crisostomo, Ane Alencar, Vivian Zeidemann, Anthony Jepson, Lianne Jepson, Lais Guerra, Jesse Kreye, Marina Londres, Wendy Francesconi, Melanie Medeiros, Mathew Graham, and Natalie Richardson for their support and friendship.

Thanks to Ana Tereza Vital.

I also would like to thank all the people who, to a greater or lesser extent, participated on our Brazilian music project, which has filled my life with joy and eased the difficulties along the way.

I'd like to thank the people with whom I grew up and to whom I always return for strong friendship during good times and bad times, "*Valeu Galera do Gantois!*"

Thanks to Abel Conceição from the Universidade Estadual de Feira de Santana in Bahia, who initiated a much needed research program on the fire ecology of the Chapada Diamantina and supported my initial research projects in that region.

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LIST OF ABBREVIATIONS

BA	Basal area in meters squared
CCTF	Closed canopy tropical forest
dbh	diameter at breast height

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

FRUIT FALL PATTERNS IN AN EXPERIMENTALLY BURNED AMAZONIAN FOREST

By

Eric Oliveira Carvalho

August 2011

Chair: Leda N. Kobziar

Major: Forest Resources and Conservation

Wildland fires in Amazonian forests have increased over the last 20 years, being linked to droughts and coupled with anthropogenic land use and ignitions. The aftermath of forest fires is generally a reduction in species richness, live stem density, and tree biomass, as well as increased litter input, canopy openness, and tree mortality rates. Fire-related tree mortality not only influences the future flammability of burned forests but can affect several ecosystem processes that are more elusive to track than the immediate effects of burning. Among these processes there are those related to tree reproduction and forest recovery. The present study addresses fruit-fall patterns in an experimentally burned tropical forest in an attempt to shed some light on the effects of fire on these processes.

This study was undertaken within a large scale fire experiment in an Amazonian Transitional forest. The experiment consisted of one experimental unit divided into three 50 ha plots. Treatments consisted of a plot burned two times in five years (B2), a plot burned four times in five years (B4), and a control (never burned B0). Fruit-fall data was gathered in a series of traps (252) systematically placed within the plots. Traps were sampled twice monthly but for the analysis data was scaled to yearly periods. Linear

mixed effects models were used for data analysis. In addition to evaluating the sole effect of fire, fruit-fall patterns were also linked to tree and liana density, basal area, diversity, and distance from the forest-agriculture edge.

Fruit-fall mass was higher in B4 than in the control at longer distances from the forest edge. Plot B2 and B0 did not differ in this regards. Species richness in fruit-fall was higher in B2 at higher tree and liana densities. Plots B4 and B0 did not differ from the control or from the two times burned plot in this regards. Both results are in contrast with our initial expectation that fruit-fall mass and species richness would decline with the fire treatments.

CHAPTER 1 INTRODUCTION

Over the last two decades, fires in tropical closed canopied forest have emerged from a virtually unrecognized phenomenon to a serious threat to biodiversity and resources. While there is growing evidence of the enduring presence of fire in the histories of tropical forests, with potential contributions to the maintenance of biodiversity (Sanford et al. 1985), the severity and frequency with which modern fires burn in tropical forests is alarming. Furthermore, unlike historic tropical forest fires, emergent fire patterns are thought to be mostly a result of human alteration of tropical forests coupled with abundant ignition sources in the form of resource management and extraction fires. The alteration of forest cover (through deforestation) and forest structure (principally through logging) by human land use affects several characteristics of tropical closed canopied forests that formerly conferred some degree of immunity to burning (Uhl and Kauffman 1990, Holdsworth and Uhl 1997, Ray et al. 2005). The aftermath of forest fires is generally a reduction in species richness, live stem density, and tree biomass, as well as increased litter input, canopy openness, and tree mortality rates. These effects and their extents are dependent on forest location and fire history. Fire-induced stem mortality, for example, ranges from 8% to 23% in Amazonian transitional forests, while for Central Amazonian forests mortality range from 36% to 64% (reviewed in Barlow and Peres 2006a).

The severity of tropical forest fires has been attributed to the fact that tropical trees are poorly equipped to cope with burns. In particular, the bark of most species poorly protects their cambium from lethal fire temperatures (Uhl and Kauffman 1990). The large number of trees killed by fires creates openings in the canopy allowing more

sunlight to reach the forest floor, increasing temperatures and decreasing fuel moisture contents (Uhl and Kauffman 1990, Holdsworth and Uhl 1997, Ray et al. 2005). Thus, as with logging and other forest-damaging practices, fire renders burned forests more prone to subsequent fires (Cochrane and Schulze 1999, Cochrane et al. 1999). Debris from dead trees adds to the fuel loads of burned forests, which are generally higher than those found in un-burned areas (Uhl and Kauffman 1990). Second and third burns have been reported to be of higher intensity and severity thus further degrading affected forests (Cochrane et al. 1999, Cochrane 2003).

Fire-related tree mortality not only influences the future flammability of burned forests but can affect several ecosystem processes that are more elusive to track than the immediate effects of burning. Among these processes there are those related to tree reproduction and forest recovery. With growing concern over increased forest fires in the Amazon Basin, we need to understand the factors that determine the capacity of fire-affected forests to recover species diversity and biomass. Tropical forest recovery after burning is certainly a slow process as is with other severe disturbances (Chazdon 2003). In addition the regeneration is likely to be strongly dominated by species capable of sprouting following above-ground mortality. Sprouting is an important means by which many species recover after cutting, though cutting followed by burning dramatically decreased the number of sprouts (Uhl et al. 1981). After disturbances of varying intensities, including high and low intensity fires, Kennard et al. (2002) observed that sprouts were the dominant form of regeneration in a transitional forest in the Bolivian Amazon. In contrast, Kauffman (1991) found that 39 - 69% of the top-killed trees in a burned Amazon forest did not sprout eight months after fire, and that 41% of

the 125 species studied lacked the capacity to sprout. In addition, fires can decrease the amounts of viable seeds in soil seed banks by 50 to 94% in low intensity and high intensity burns, respectively (Kennard et al. 2002). This realization implies that seed dispersal into burned areas is likely to be an important means by which burned forests can recover. Repeated burns, however, further complicate the picture, because subsequent fires kill sprouts and seedlings, damage seed banks, and kill trees that would otherwise contribute seeds. In repeatedly burned Amazonian forests, understory regeneration after fire is dominated by herbaceous species that suppress woody plant regeneration (Barlow and Peres 2008).

Fruit production in burned forests has not been addressed extensively. Fruits and the seeds they contain play a major role in the dynamics of tropical forest plant and animal communities by acting as reproductive resources for the former and food for the latter. These functions work hand in hand as many tropical plant species produce animal-dispersed seeds that make up a substantial portion of several wildlife species' diets. In some tropical forests, for example, the tree flora may be comprised of up to 95% zoochorous species (Peres and Roosmalen 2002). By influencing fruit production, fire can have a profound effect on plant recovery and wildlife populations. Barlow and Peres (2006b), demonstrated that fires depressed the basal area of fruiting trees. The authors also demonstrated that despite a community-wide reduction in fruiting tree basal area, not all species presented decreased number of fruiting stems. Barlow and Peres' study was the only one we found that specifically addressed post-fire fruit production, though their study did not measure fruit production directly.

The study of reproduction in tropical forests is in itself a difficult enterprise in that these forests usually contain numerous tree species that occur at low densities and employ different reproductive strategies. This implies that reproductive phenomena in tropical forests are spatially and temporally heterogeneous, requiring large areas and long periods of time sampled to provide a glimpse into their dynamics. Furthermore, baselines to compare disturbed and undisturbed forests are scarce (Barlow and Peres 2006a). Thus it is no surprise that few studies have addressed the consequences of fire for plant reproduction in closed canopy tropical forests.

We present data on the effects of fire on fruit-fall patterns of experimentally burn plots on the southern edge of the Amazon Basin. Our aim was to assess the effects of repeated burns on temporal patterns of fruit-fall. The treatments applied to 50 ha plots consisted of a plot burned twice in five years (B2), a plot burned four times in five years (B4), and a plot never burned (B0, no signs of recent burning). As different burning intervals have been shown to influence fire behavior and tree mortality, we assessed differences among these treatments. We first investigated whether fruit-fall changed over time and among treatments, subsequently relating these patterns to fire-induced changes in tree and liana density, basal area (BA), and species diversity. Furthermore, because forest fires are often associated with deforestation edges, we evaluate the combined effect of fire and distance from the edge on fruit production. Edges influence both tree mortality patterns and fire behavior (reviewed in Laurance 2006). Higher temperatures, insulation, and wind exposure create edge environments that favor rapid fuel dry down rates. Higher tree mortality rates and litter input on edges insure higher fuel loads in these areas that in association with drier conditions, lead to fires of higher

intensity in edges than in forest interiors. In addition, invasion of pasture grasses can occur into edge environments with substantial effects on fire behavior (Balch et al. 2009, Veldman et al. 2010). The differences in fire intensity associated with forest edges may have a profound influence on tree mortality that in turn can affect fruit production. Our expectations are in conformity with those of Barlow and Peres (2006b), who argue that given the severity of Amazonian forest fires, with substantial reductions in tree density and BA, fruit production is likely to decline in burned forests when compared to unburned forests.

CHAPTER 2 MATERIALS AND METHODS

Study Site and Design

This study was conducted on Taguru Ranch, a privately owned land-holding of ~80,000 ha with transitional forest only 30 km north of the Brazilian savannas (*cerrado*) in the state of Mato Grosso (Figure 2-1; 13°01' S, 52°23' W). Located on the southern edge of the Amazon Basin, the study site falls within a broad transition zone between the Amazonian forest and *cerrado* biomes. These forests share plant species with both the *cerrado* and the wetter closed canopied forests of central Amazonia. Our study forest, for example, has at least 23 species in common with the *cerrado* to the south (Balch et al. 2011) and 45 species with the wetter forests of the Ducke reserve near Manaus, Brazil (Balch unpublished data). Compared to central Amazonian forests, transitional forests harbor fewer species, are shorter, and support less leaf area. In addition, the study area experiences seasonal droughts from May-September, with a mean annual precipitation of 1740 mm for 2004 and 2005 (Balch et al. 2011).

Within the property's legally protected forest reserve along a forest-agriculture edge (Figure 2-1), one 150 ha (1.5 x 1.0 km) experimental forest block was located. The study block is surrounded on the three other sides by at least 1000 m of un-broken forest, and has not experienced logging or burning in the recent past. The deforested side is currently used for soy cultivation but was formerly pasture. The three 50 ha (0.5 x 1.0 km) treatment plots established within the experimental block (Figure 2-2.A) consisted of a control (B0; never burned), a twice burned plot (B2, burned twice in five years), and a four times burned plot (B4 burned four times in five years). The B4 burn plot was not burned in 2008.

Experimental Fires

The first burn of both experimental plots was in September 2004 with subsequent burns also near the end of the dry season (August-September). Fires were lit as strips following the north south trails, and each burn plot took 2 - 3 days to be completed (Balch et al. 2008 for more details on experimental fires).

Floristic Survey

Prior to the first burn every tree with diameter at breast height (DBH) ≥ 40 cm in each plot was mapped, tagged, and measured for height and DBH (stem diameter at 1.30 m). Trees and lianas 20-40 cm DBH were sampled in belt transects (500 x 20 m) 0, 30, 100, 250, 500, and 750 m from the forest-agriculture edge (i.e., 5.5 ha sampled per 50 ha treatment plot). Trees and lianas 10-20 cm DBH were sampled within smaller transects (500 x 4 m) nested in the larger ones (Figure 2-2). All marked trees and lianas were revisited prior to each burn to assess mortality and any new individuals that recruited into the considered size classes were surveyed.

Fruit-fall

Fruits were collected from a series of 0.5 m² traps placed systematically throughout the experimental plots. Traps were located 5 m outside of the forest in the agricultural clearing and 50 m apart at 0, 15, 30, 50, 100, 250, 500, and 750 m (north-south) from the edge (Figure 2-2.A). A total of 270 traps were deployed in the 150 ha area, 90 per treatment. Traps bordering two treatment plots (i.e. traps in B2 but close to B0 and those in B4 but close to B2) were excluded from analysis. In total 18 traps were excluded. These traps were considered to be too close to other treatment plot as they were located less than 10 m from the edge of two treatment plots. Their proximity to two treatment edges makes them prone to be influenced by trees within two different

treatment plots (Figure 2-2.A). In total, therefore, the actual number of traps used for analysis was 252 (90, 81, and 81, for plots B0, B2, and B4 respectively). All traps were visited at ~two week intervals starting after the fire in September 2004 and continuing through September 2009. Fruits and seeds in the traps were identified to the lowest taxonomic level possible, counted, oven dried, and weighed.

Forest Structure and Diversity Analysis

The analysis of the effects of fire over forest structure and diversity was conducted descriptively by the interpretation of graphs. The combined effects of fire and distance from the forest edge on tree and liana density, BA, and diversity in trap-centered plots was analyzed through graphs, and correlation analysis, assuming a linear relationship among the variables. For this portion of the analysis data was grouped by year and treatment and correlation values were assigned to each treatment year combination with distance from the edge being an explanatory covariate. For this analysis we sought to determine whether the linear relationship between the measures of forest structure and diversity and distance from the edge were affected by repeated fires.

Fruit-fall Data Analysis

Data analyses included both qualitative interpretation of graphs and quantitative assessments with inferential statistics. Analyses were conducted at the community level with all species in the fruit-fall pooled. Community-level analyses included fruit-fall species richness and fruit-fall mass. In the statistical analyses the unit of observation was the trap and the observation period the year, and fruit/seed dry-weight was used as the measure of production. Traps were sampled repeatedly; therefore, to account for the repeated measurement structure of the experimental design, mixed modeling

methods were used that specifically accounted for the correlations among measurements taken on the same experimental unit (the trap).

We used dry-weight as the measure of production because fruits were not distinguished from seeds during the processing phase. For example, if an intact fruit contained three seeds it would be counted as one but if the same fruit was opened and the seeds exposed it would be counted as three. For the purpose of this study we refer to the dry-weights of reproductive material (i.e., fruits and seeds), as fruit-fall mass. We recognize that there are issues in utilizing dry weight as the measure of production, the most obvious of which is the fact that a great majority of studies of seed/fruit fall report their results in terms of numbers of seeds. Furthermore using dry-weight may over-emphasize species with large heavy fruits over those with smaller, lighter fruits. Conversely, using number of seeds as the response variable over-emphasizes species that produce large numbers of small seeds.

All statistical analyses were conducted on a yearly basis because we intended to relate fruit-fall and measures of forest structure and diversity. As floristic data were acquired on a yearly basis, we scaled the fruit-fall observations to yearly periods starting in August when experimental fires were conducted.

Tree and liana survey data were used to create a series of variables that included BA, density, and Shannon's diversity index. The relationship between these variables and fruit-fall were explored graphically and also used as covariates in the analysis of fruit-fall. Given that the experimental plots are relatively large units in comparison to each trap, rather than assigning one value per year per treatment for each explanatory variable, we assigned a unique value for each variable to each trap.

To assess local conditions, trees and lianas within 30 m of each trap were used to calculate structure and diversity variables for each year (Figure 2-2.B). Having tested radii, ranging from 20 m to 70 m, we selected a 30 m radius on the basis of the largest correlation (Pearson's product moment correlation coefficient) between explanatory and response variables. The choice of the 30 m radius plot is also supported by the fact that most fruits tend to disperse close to the parent plants with a rapid decrease in density with increasing distance. For example, Godoy and Jordano (2001) found that for the zoochorous *Prunus mahaleb*, in Spain, up to 62% of the seeds arrived within 15 m of the parent tree, while also dispersing seeds to distances up to 316 m.

The present study has two major experimental design challenges. The first is lack of true replication as there is only one plot per treatment and using traps as replicates therefore represents pseudo-replication (Hulbert 1984). Nevertheless we used inferential statistics as recommended by Oksanen (2001), who advises that inferential statistics can assist with the observation of patterns particularly where comparison of time trajectories among treatments is sought. The second deficiency is that fruit-fall data collection only commenced after the first burn so we must assume that the fruiting patterns were similar among treatment plots prior to the onset of the experiment. These deficiencies notwithstanding, the study spans a large number of years and was conducted over a large spatial scale.

Community Fruit-fall Mass Analysis

Community level fruit-fall mass analysis was primarily intended to elucidate changes in fruit-fall patterns among treatments over time. We also wanted to ascertain the relationship between fruit-fall mass and forest conditions such as tree and liana density, BA, and distance from the forest-agriculture edge. Given our main objectives,

we devised a statistical model that contains independent variables and interactions that we believe are appropriate to answer questions posed. Thus we initiated our model selection with the following fixed effects: treatment, year, distance, density, treatment x year, Treatment x distance, year x tree and liana density, year x distance from the edge, treatment x year x density, and treatment x year x distance. This model was considered the “global model” (Burnham and Anderson 2002) from which several nested models were derived for comparison. We also determined that any model analyzed would at least contain the variables year, distance, and density. We did this because previous work on fruit production suggests that these variables have strong influences on community reproductive output. In addition we chose to utilize only one measure of tree and liana abundance in models, since there is high correlation between Density and BA ($r=0.80$, $p<0.001$).

The most parsimonious model was selected on the basis of Akaike Information Criterion (AIC). As mentioned above, mixed models with a random effect for year and trap were used. The response variable (fruit mass) was log10 transformed for this portion of the analysis.

Number of Species Reproducing

In addition to graphical interpretation, the number of species in the fruit-fall traps was also assessed through the use of linear mixed models. Covariates in this analysis included those utilized in the community analysis (see above) with the addition of Shannon’s diversity index, $H' = - \sum_i p_i \log_b p_i$, where p_i is the proportional abundance of species i , and b is the logarithm base. As in the analysis of fruit-fall mass, we utilized model selection procedures to arrive at a model that best explains the data.

The global model for species richness of fruit-fall contained the following simple effects: treatment, year, density, distance, and diversity (Shannon's index). The model also contained the following interactions: treatment x (year; density; distance; diversity), year x (density; distance; diversity), treatment x year x (density; distance; diversity). Model selection was conducted by removing model terms until the models contained at least year, density, and distance as explanatory variables. As with fruit-fall mass, we selected the model to further analyze the number of species in fruit-fall using AIC.

Mixed models were also structured with random effects for year and trap. All analyses were conducted in R (R Development Core Team 2010), and the following packages were extensively used: ggplot2 (Wickham 2009), lattice (Sarkar 2008), nlme (Pinheiro et al. 2010), doBy (Hojsgaard et al. 2010), vegan (Oksanen et al. 2011), and lme4 (Bates and Maechler 2010).

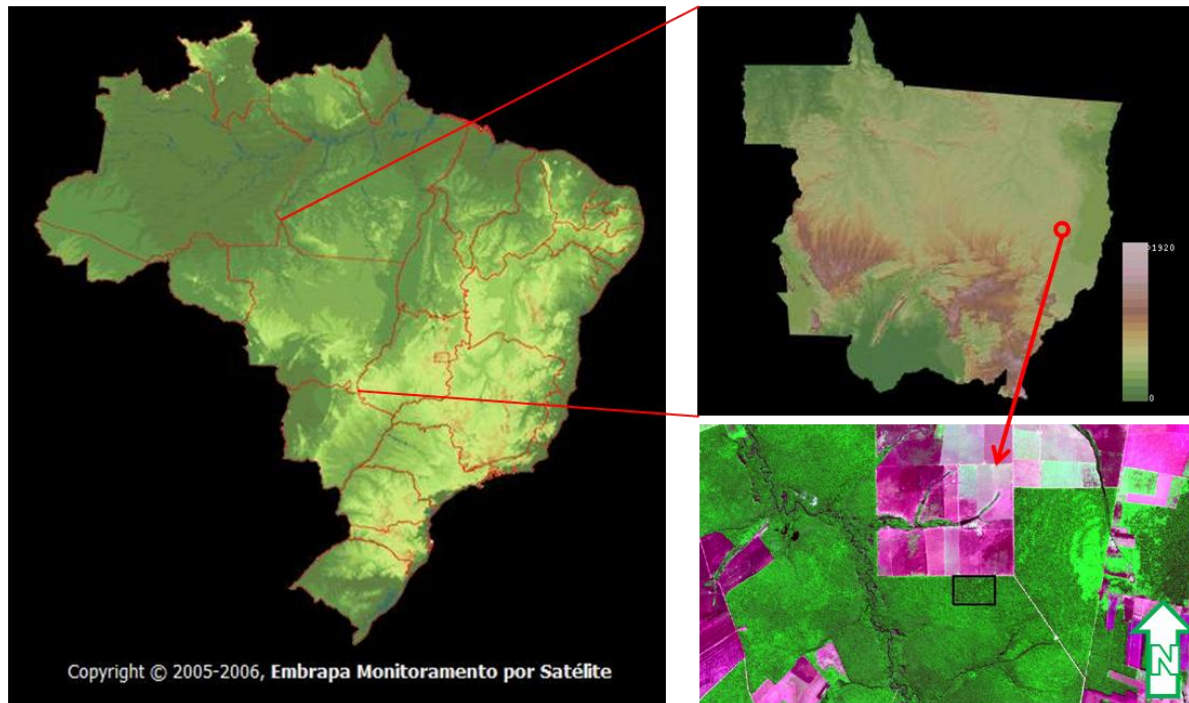


Figure 2-1. Study site location. Tanguru Ranch, State of Mato Grosso, Brazil, lower right image shows the experiment block (black rectangle) surrounded by forest on three sides and edging an agriculture field on the north.

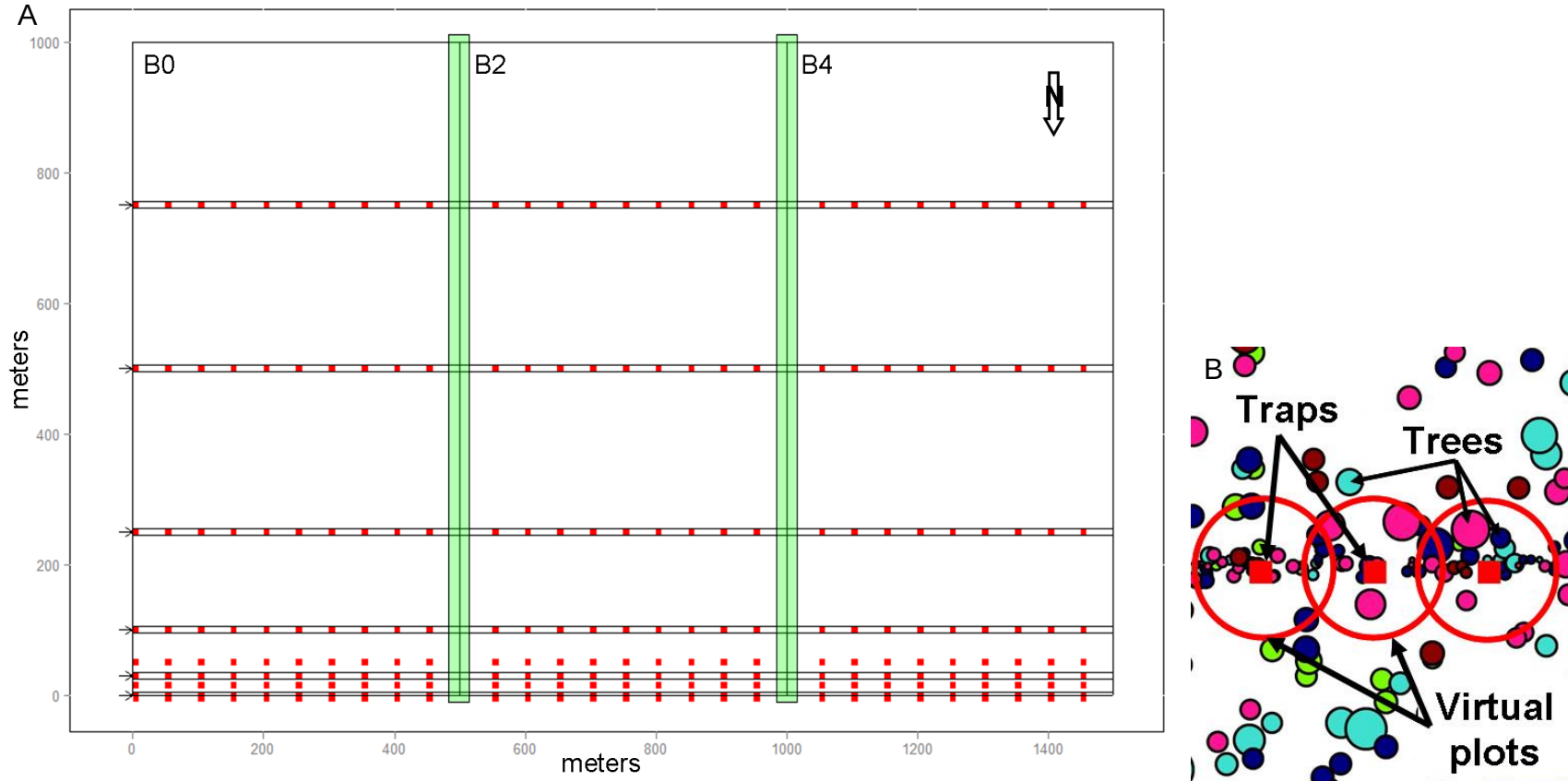


Figure 2-2. Spatial arrangement of experimental plots, distribution of traps (red squares) and floristic survey transects (indicated by small arrows on the left margin; A). The green rectangles show areas from which traps were excluded due to proximity of two treatments. B) A sample map of three trap-centered plots; red squares represent traps, open red circles the perimeter of each plot, and solid circles trees.

CHAPTER 3 FIRE AND EDGE EFFECTS ON FOREST STRUCTURE

Tree and Liana Density, Basal Area, and Diversity in Trap-centered Plots

As revealed by descriptive analysis the data, fire caused decreases in tree and liana densities near the traps in both fire treatments especially after the 2007 fire, with a more pronounced fall in B2 (Figure 3-1). The mean density per trap-centered plot in B2 was initially 24.9 (standard deviation (sd)=9.9), fell to 10.6 (sd=10.6) in 2007-2008, and remained relatively constant at 10.4 (sd=10.2) the following year. Similarly, tree and liana density in B4 steadily fell to 56% of its 2004-2005 survey by 2008-2009. The mean tree and liana density per trap-centered plot in 2004-2005 in B0 was 24.8 (sd=8.9) but by 2008-2009 was 21.2 (sd=8.7), a decrease to 85.73% of its 2004-2005 survey amount. In concert with declines in tree and liana density, basal area of trees and lianas also showed a substantial decline in the burned plots after the 2007 fire, especially in B2 (Figure 3-2). Both tree densities and BA remained relatively constant after their decline following the 2007 fire.

Lower diversity of trees and lianas in trap-centered plots (Shannon's index, H') was associated with fire treatments, with a more pronounced fall in B2 than B4 (Figure 3-3). Mean H' for B2 was 0.37 (sd=0.14) in 2004-2005 and fell to 0.20 (sd=0.19) in 2008-2009. On B4, mean H' was 0.43 (sd=0.11) in 2004-2005; it decreased with subsequent fires with a pronounced decrease in 2007-2008 when it reached 0.29 (sd=0.17), and subsequently fell to 0.27 (sd=0.18) in 2008-2009. The control plot (B0) maintained a relatively constant diversity in trap centered plots throughout the experiment with a mean H' of 0.39 (sd=0.13) in 2004-2005 that dropped slightly to 0.35 (sd=0.15) in 2008-2009.

Distance From the Edge Effects on Tree and Liana Density, Basal Area, and Diversity

Tree and liana density in trap-centered plots was positively correlated with distance from the forest edge, both with all treatments and years pooled and by treatment and year separately (Figure 3-4). With treatments pooled, distance was weakly correlated with tree and liana density ($r=0.42$). When grouped by treatment and year low, correlation values were observed, but increased after 2007-2008 in B2 (Table 3-1). In addition, fire appears to have influenced the relationship between density and distance from the edge, as intercepts show a decreasing trend while slopes show an increasing trend with repeated burns (Figure 3-4 and Figure 3-5). The decline in intercepts indicated that the mean density in trap-centered plots at the forest edge decreased with time and fires. The increasing slopes show that fire caused the relationship between density and distance from the edge to become steeper. That is density tended to increase with distance at higher rates with passing years and subsequent fires. This effect was more apparent in B2 than B4; while intercepts in B4 decreased, slopes did not increase as in B2.

Tree and liana basal area in trap-centered plots followed the same trend as density, increasing with distance from the forest edge (Figure 3-6). Distance was only weakly related to changes in basal area with treatments and years pooled ($r=0.41$). With data grouped by treatment and year the correlation between BA and distance from the forest edge varied greatly depending on treatment and year, remaining weak, however, in the control and B4 treatments but increasing in B2 after 2007-2008. Furthermore, as with density, fire appeared to influence the relationship between basal area and

distance causing a decrease in intercepts both for B2 and B4 and increase in slopes, especially in B2 (Figure 3-7).

The diversity of trees and lianas in trap-centered plots also was positively associated with distance from the forest edge, though this relation was weak (Figure 3-8). For all treatments and years, distance from forest edge was weakly correlated with H' ($r=0.30$). In addition, with data grouped by year and treatment, the coefficient of determination remained low but tended to increase with time (Table 3-3). Of the three treatments, B2 had the highest increase in correlation with years, particularly after 2007-2008. The intercepts and slopes of the relationship between H' and distance from the edge showed similar tendencies in all treatments, the intercepts declined while slopes increased with years (Figure 3-9). In the control these tendencies were not apparent as observed by both intercepts and slopes and their confidence intervals. In contrast, B2 and B4 intercepts declined after 2007-2009. Only for B2 was the slope increase over time and treatment substantial.

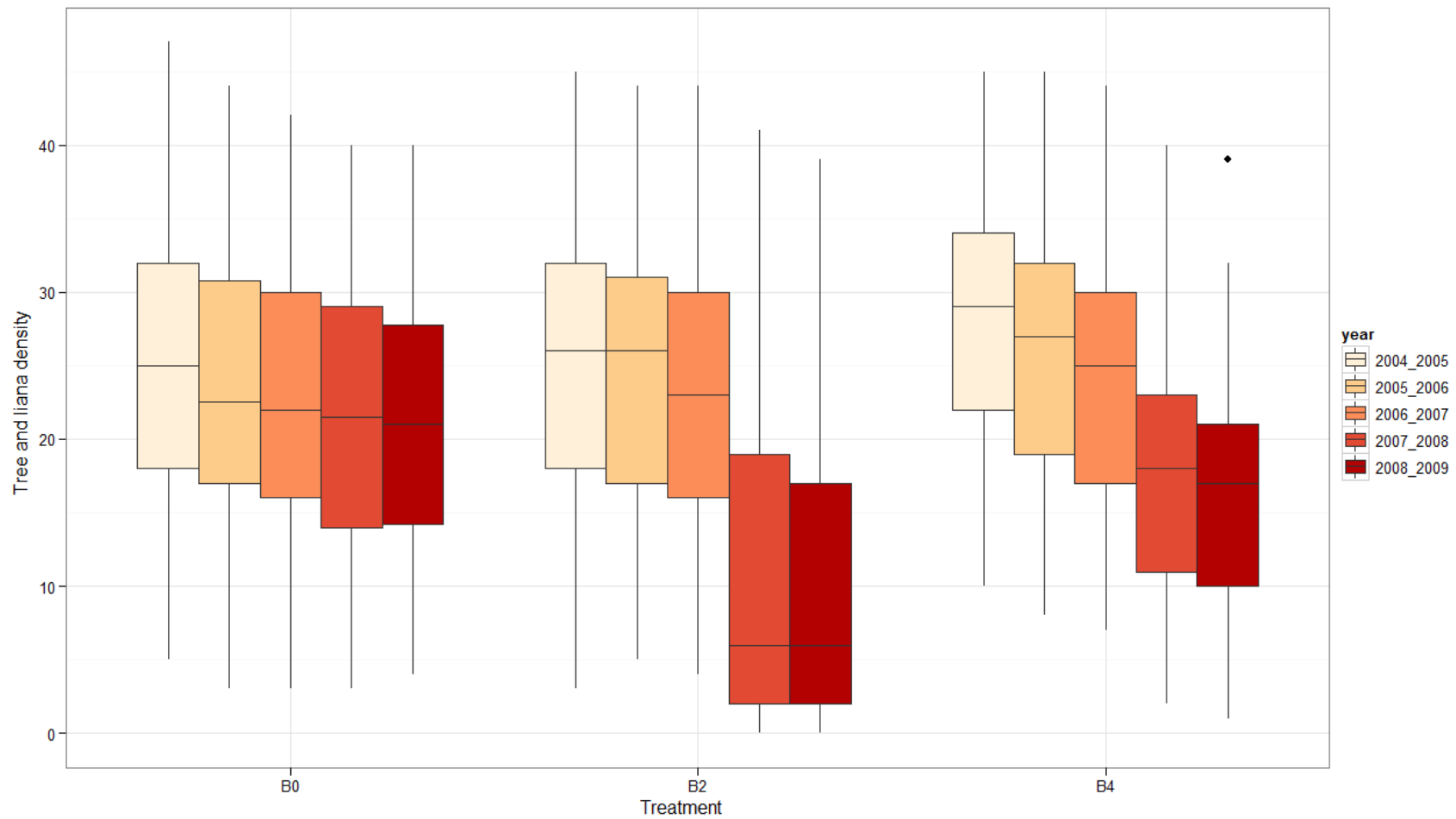


Figure 3-1. Boxplots of tree and liana densities within 30 m of the traps for each of the five years of this study grouped by treatment and year (B0 = control, B2= two times burned, B4 = four times burned). The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles +/- 1.5 interquartile range, and “♦” are outliers.

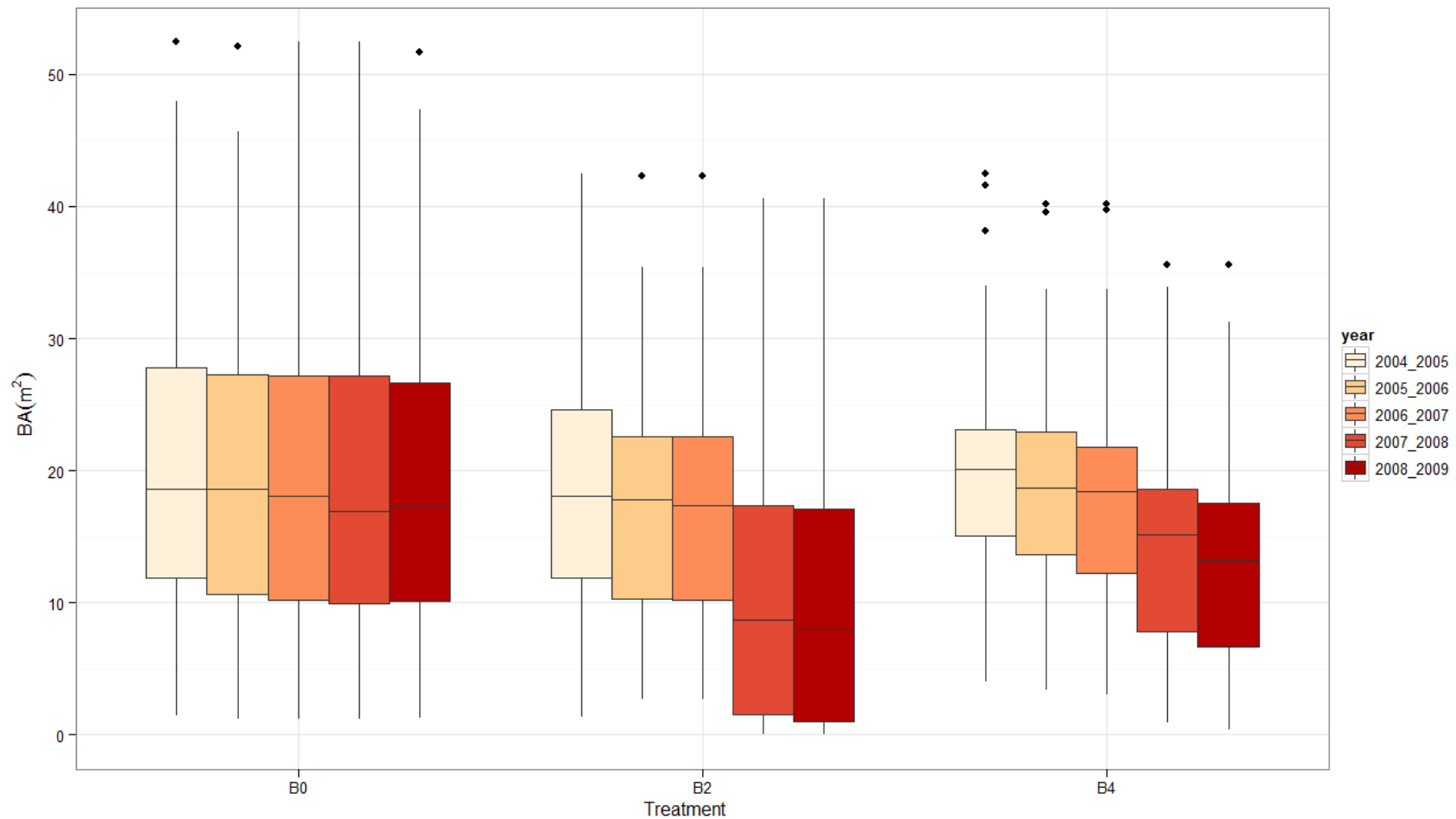


Figure 3-2. Boxplots of tree and liana basal area (m^2) within 30 m of the traps for each of the five years of this study grouped by treatment and year (B0 = control, B2= two times burned, B4 = four times burned). The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles +/- 1.5 interquartile range, and “♦” are outliers.

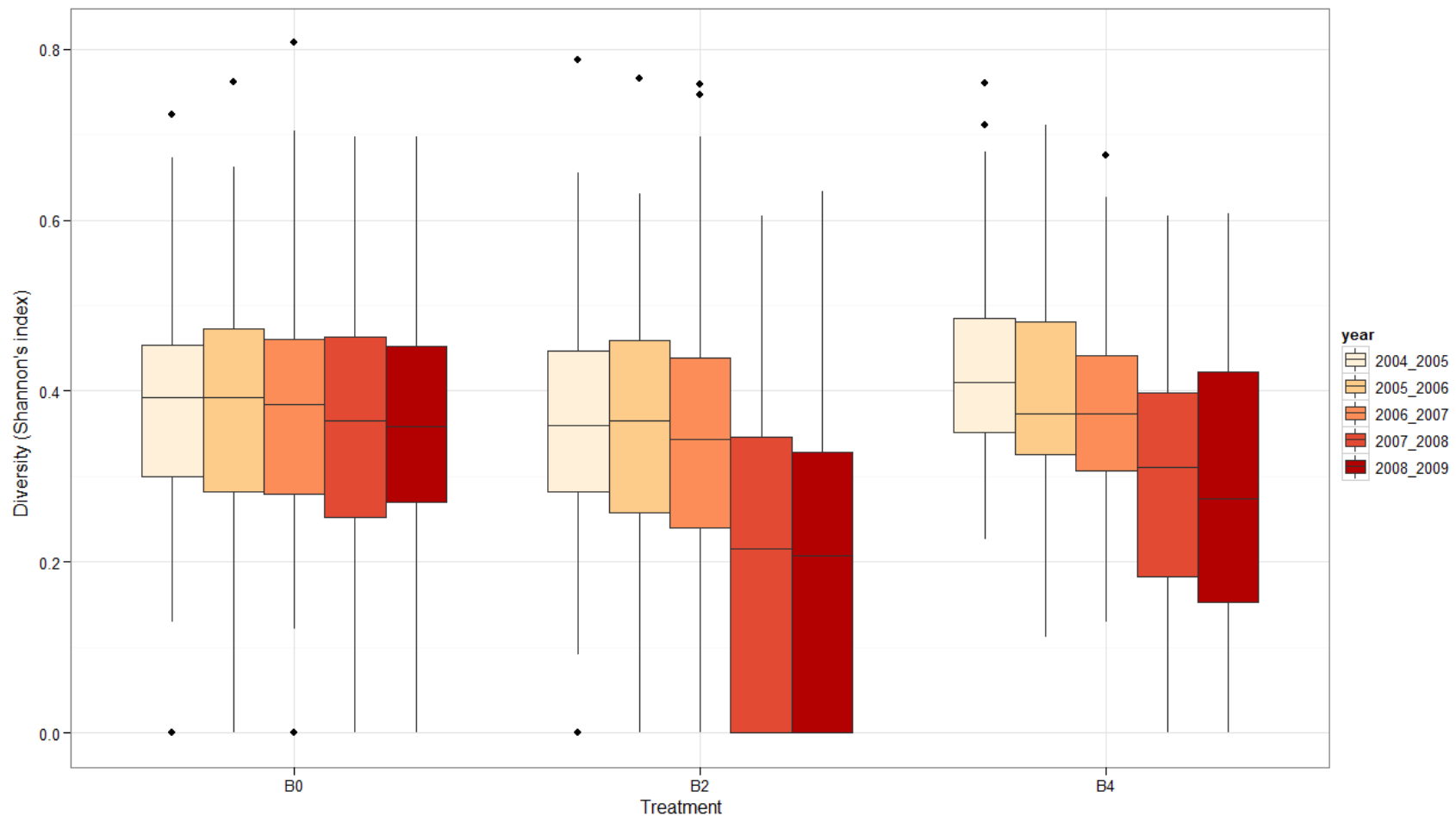


Figure 3-3. Boxplots of tree and liana diversity (Shannon's index) within 30 m of the traps for each of the five years of this study grouped by treatment and year (B0 = control, B2= two times burned, B4 = four times burned). The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles +/- 1.5 interquartile range, and "♦" are outliers.

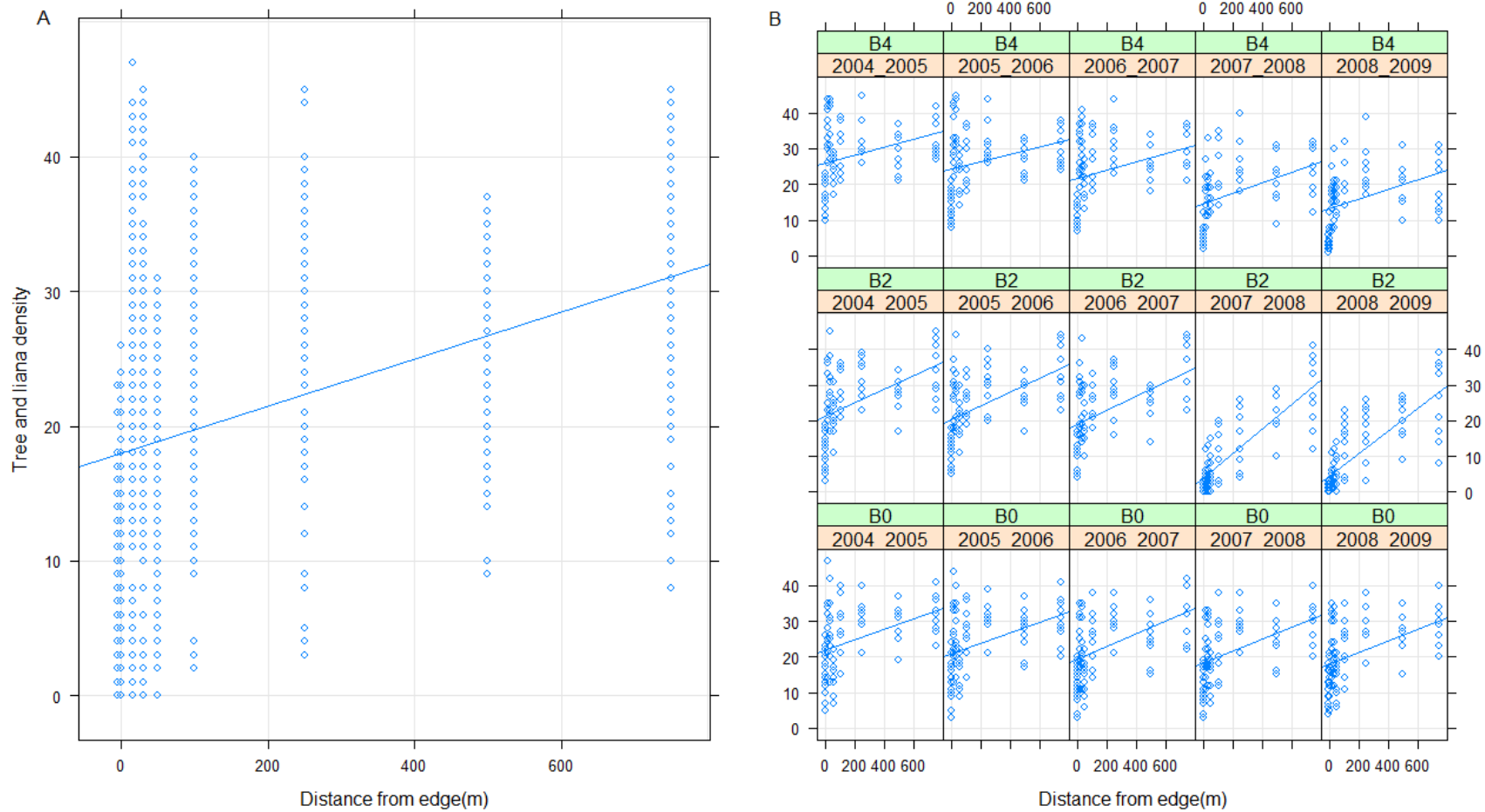


Figure 3-4. Relationship between tree and liana densities in 30 m radius trap-centered plots and distance from the forest-agriculture edge (m). A) All treatments and years pooled ($r=0.42$). B) Grouped by treatment and year.

Table 3-1. Pearson's correlation (r) values for the relation between tree and liana density in trap-centered plots and distance from the forest-agriculture edge (m) grouped by treatment and year.

	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009
B0	0.41	0.42	0.49	0.48	0.47
B2	0.47	0.47	0.52	0.82	0.77
B4	0.31	0.28	0.32	0.42	0.38

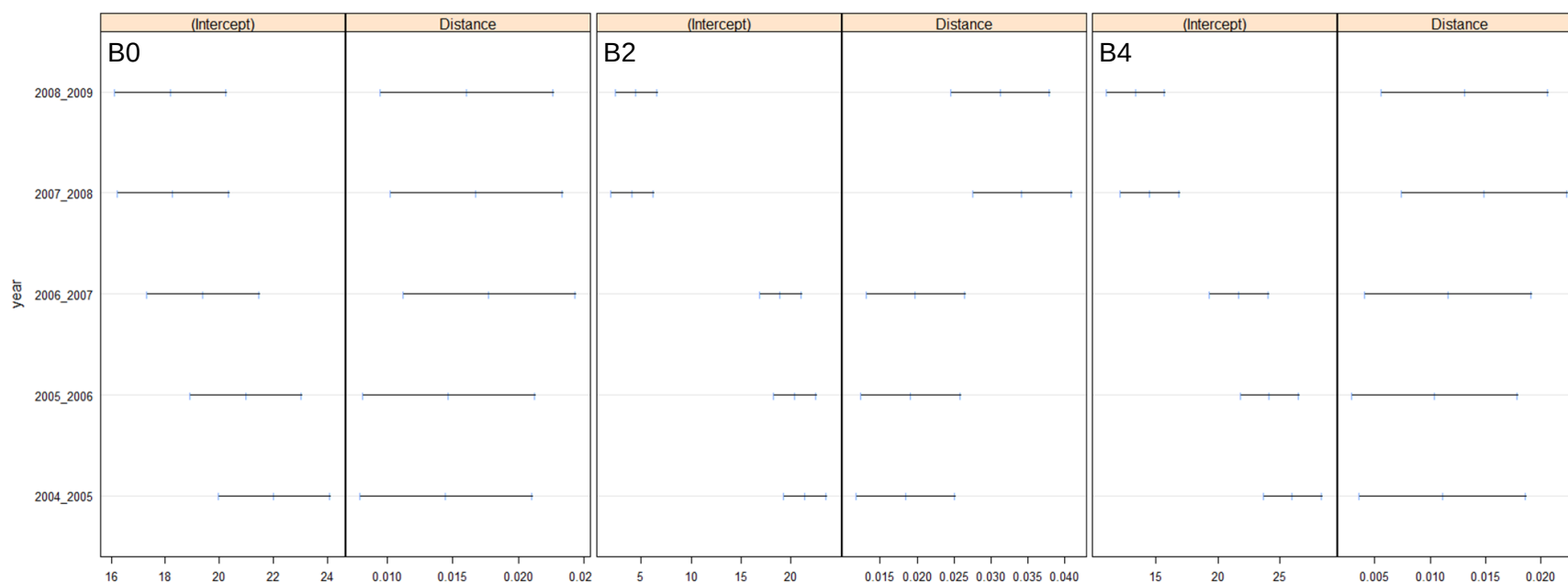


Figure 3-5. Intercept, slopes (labeled Distance), and confidence intervals for linear relations of tree and liana density in trap-centered plots by distance from the forest-agriculture edge (m) grouped by treatment and year (note that scales differ). Plotted lines represent the 95% confidence intervals with the mean in the middle.

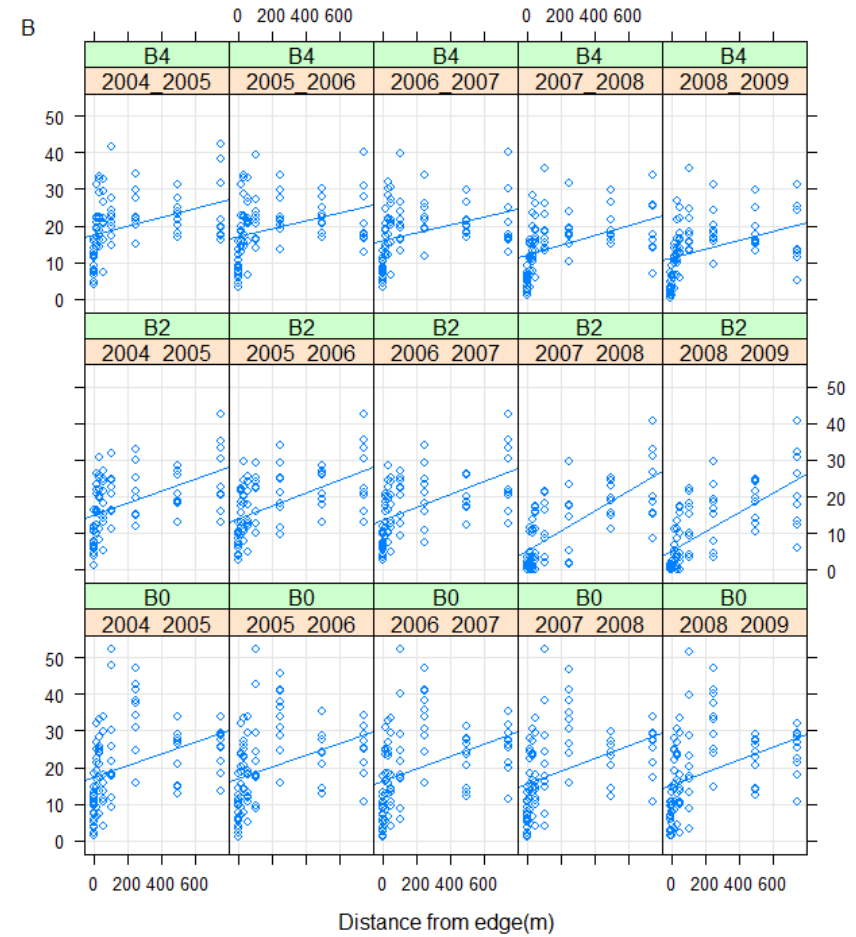
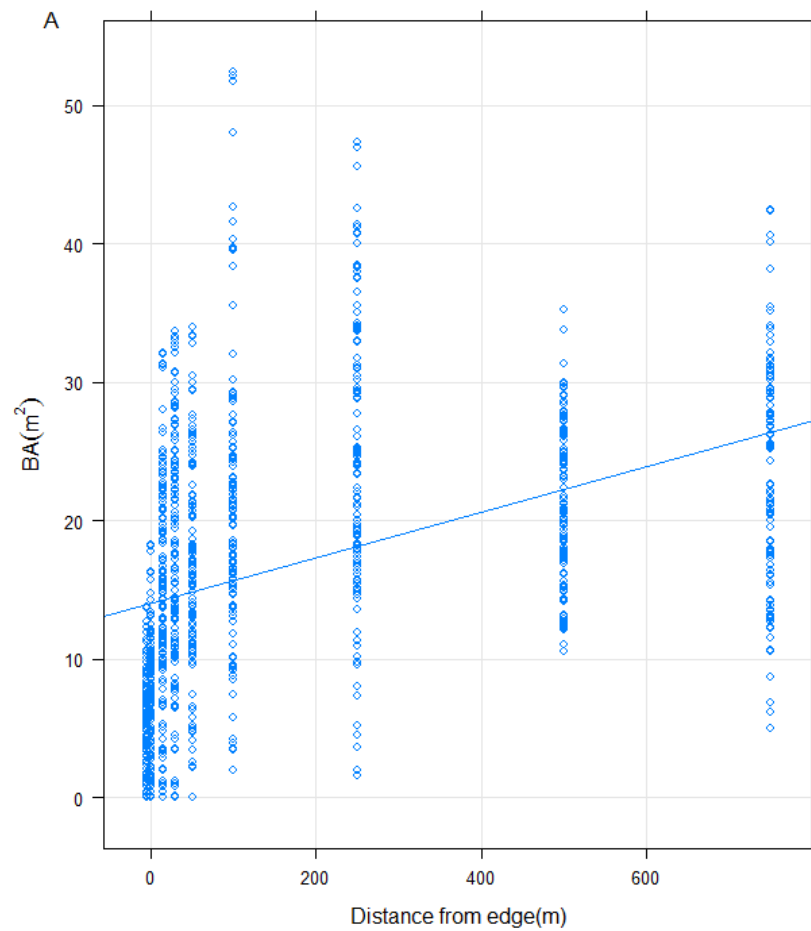


Figure 3-6. Linear relation between basal area (m^2) in trap-centered plots and distance from the forest-agriculture edge (m). A) All treatments and years pooled ($r=0.41$). B) Grouped by treatment and year.

Table 3-2. Pearson's correlation (r) values for the relation between tree and liana basal area (m²) in trap-centered plots and distance from the forest-agriculture edge (m) grouped by treatment and year.

	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009
B0	0.36	0.37	0.38	0.39	0.38
B2	0.48	0.52	0.52	0.71	0.69
B4	0.36	0.32	0.34	0.42	0.39

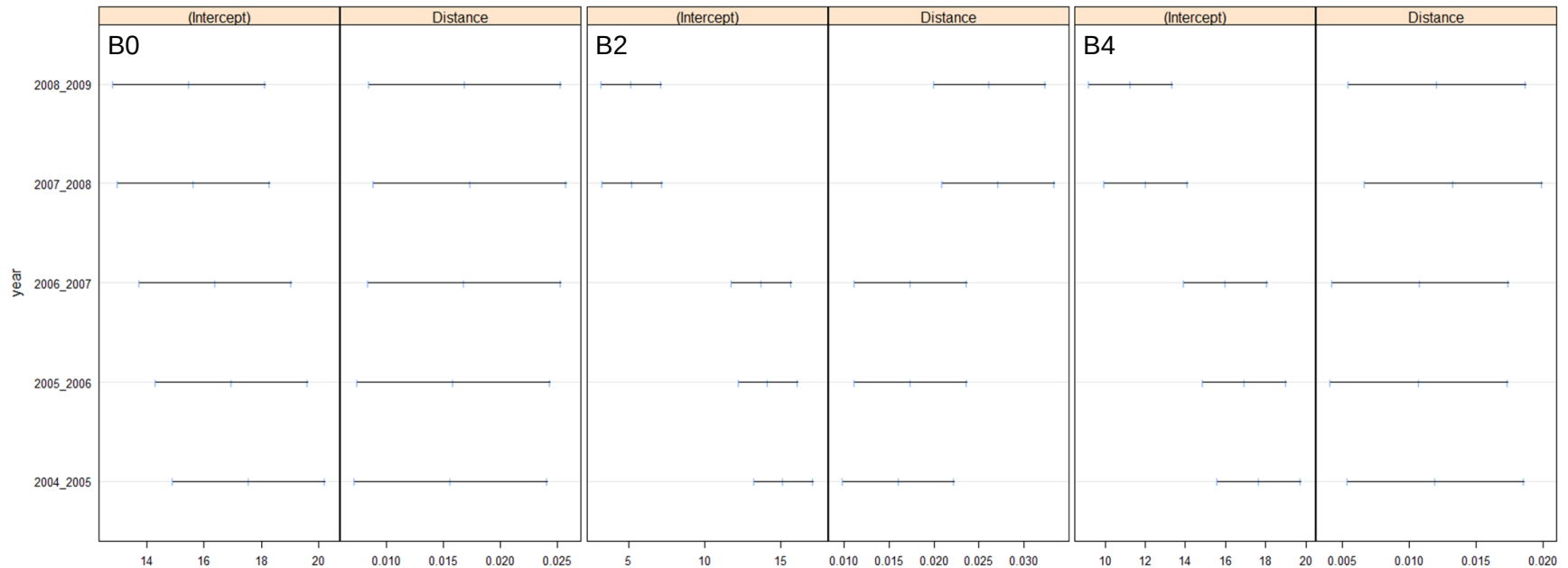


Figure 3-7. Intercept, slopes (labeled Distance), and confidence intervals for linear relations of tree and liana basal area (m²) in trap-centered plots by distance from the forest-agriculture edge (m) grouped by treatment and year (note that scales differ). Plotted lines represent the 95% confidence intervals with the mean (small dash) in the middle.

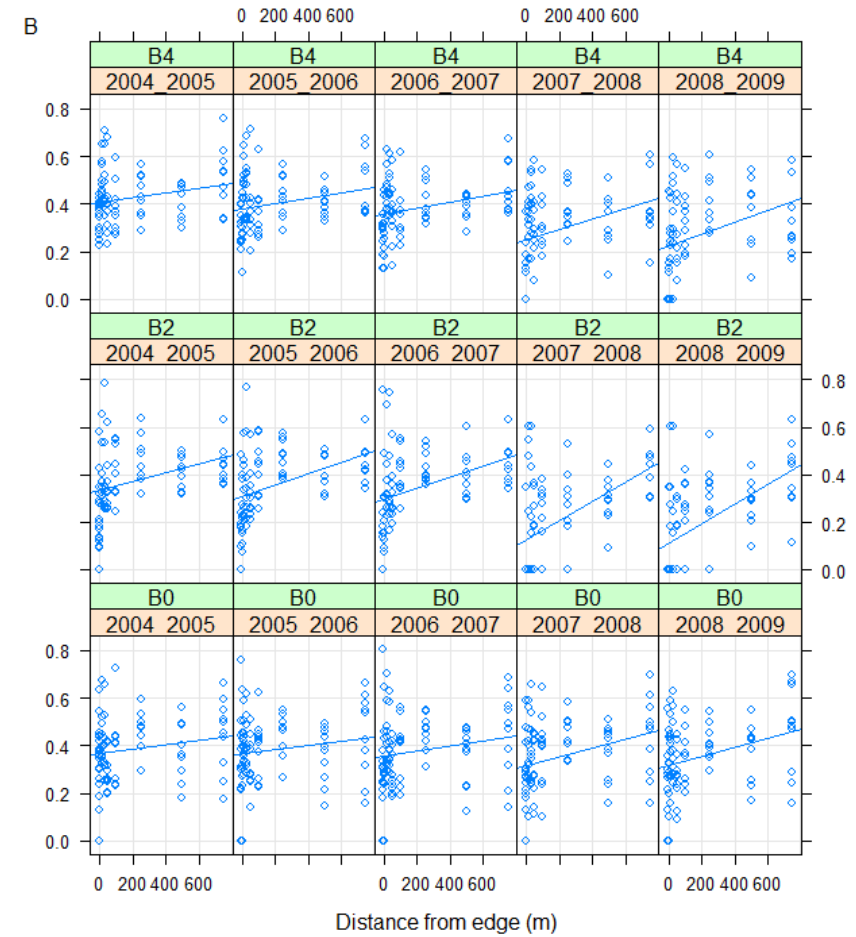
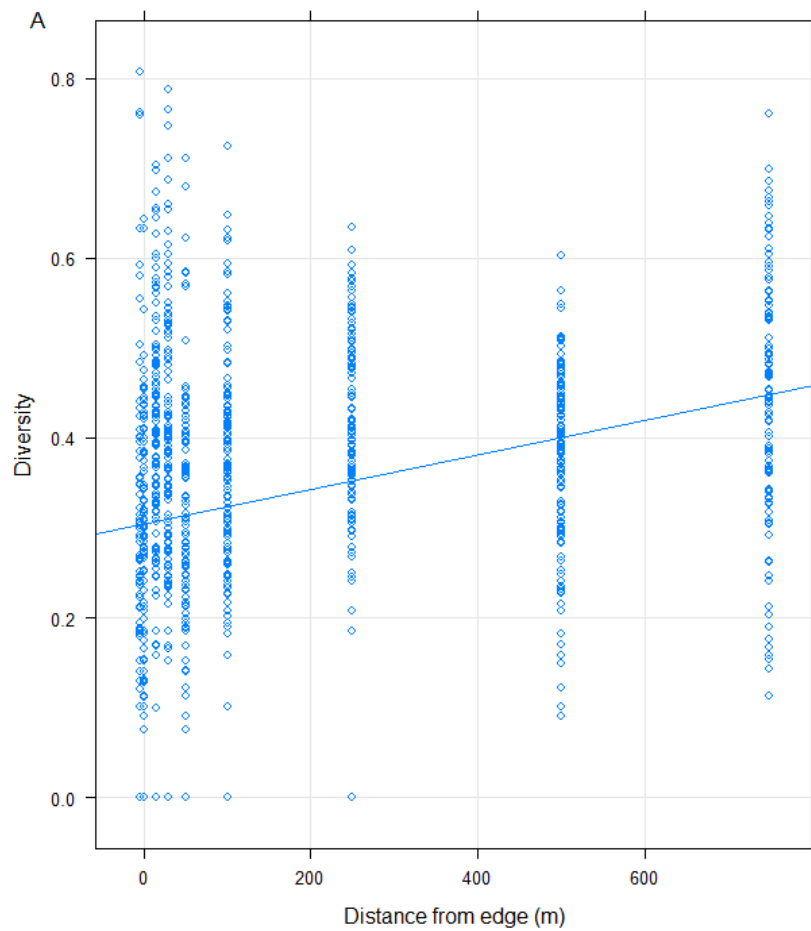


Figure 3-8. Linear relation between tree and liana diversity (Shannon's index) in trap-centered plots and distance from the forest-agriculture edge (m). A) All treatments and years pooled ($r=0.30$). B) Grouped by treatment and year.

Table 3-3. Pearson's correlation (r) values for the relation between tree and liana diversity in trap-centered plots and distance from the forest-agriculture edge (m) grouped by treatment and year.

	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009
B0	0.18	0.15	0.18	0.29	0.33
B2	0.33	0.40	0.37	0.53	0.56
B4	0.23	0.24	0.28	0.33	0.34

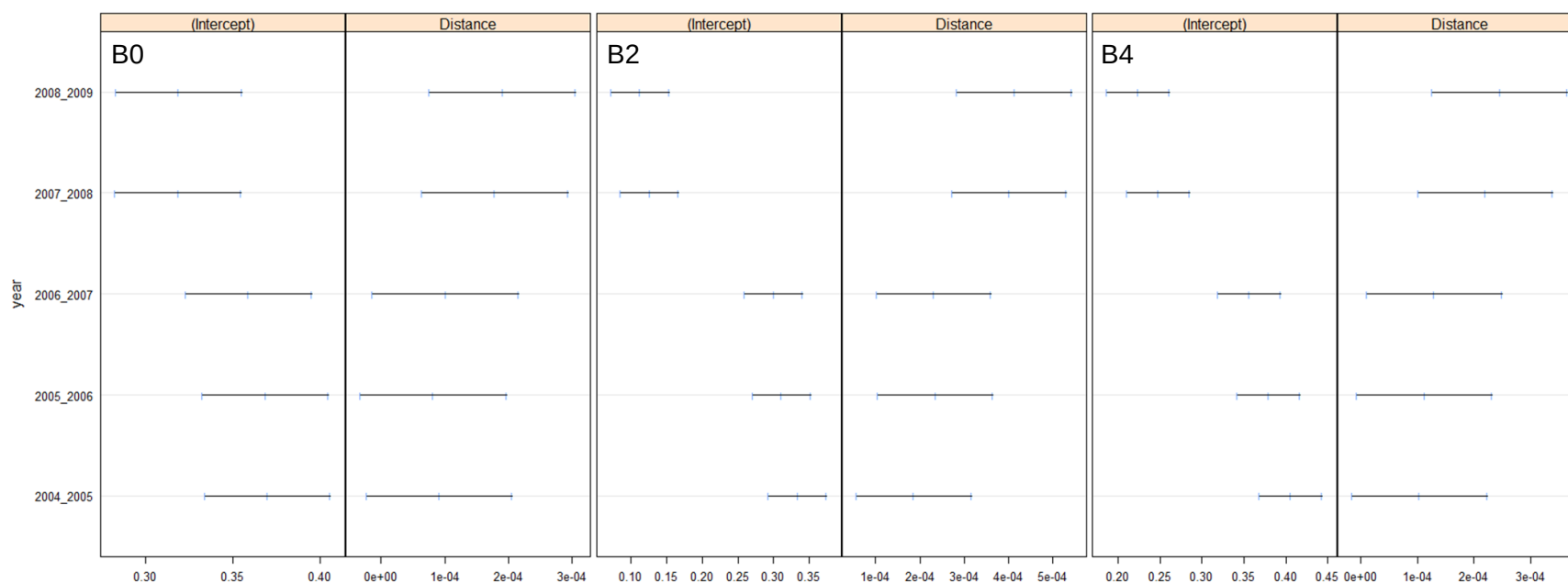


Figure 3-9. Intercept, slopes (labeled Distance), and confidence intervals for linear models of tree and liana diversity in trap-centered plots by distance from the forest-agriculture edge (m) grouped by treatment and year (note that scales differ). Plotted lines represent the 95% confidence intervals with the mean (small dash) in the middle.

CHAPTER 4 FRUIT FALL MASS RESULTS

Community-wide Results

In total 20.2 kg dry-weight of fruits were collected from the litter traps, 5.7 kg, 6.1 Kg, and 8.4 kg, in the control (B0), B2, and B4, respectively (for production on a yearly basis per treatment refer to Table 4-1). More than 50% of the fruit-fall mass produced was usually from a set of only 10 species, of which five are among the species with highest Importance Value Index (IVI) (Table 4-3). It is worth noting that among these 10 species one, *Strychnos xinguensis* Krukoff., is a zoochorous liana.

Fruit-fall Mass Patterns as Revealed by Qualitative Analysis

When considered univariately, fruit-fall mass did not appear to differ between the two burned plots and the control (Figure 4-1.B) but fluctuated substantially among years. The year 2004-2005 had the highest mass and 2005-2006 the lowest (Figure 4-1.A). Fruit-fall mass also varied considerably intra-annually, with similar general temporal patterns in all three plots (Figure 4-2). Monthly production generally peaked January-April for all years and treatments except in 2004-2005, where B2 peaked in September-October and B0 and B4 that peaked in November-December (Figure 4-2.A). Annual peaks coincided with the October-April rainy season. When considering the proportion of traps in which fruits were found, a similar trend towards more fruiting in the rainy season was observed for all treatments and years (Figure 4-2.B). Treatment B2, after the 2007 fire, consistently had lower numbers of traps with fruits than the other two treatments.

Annual total fruit-fall mass per treatment fluctuated among years similarly in the three plots except B2 in 2008-2009 (Figures 4-3.A and B), during which its traps

collected only 795 g, which was less than half as much as that collected in B0 and in B4 for that year. By contrast, over the previous four years, B2 production was: 66%, 31%, 30%, and 13% higher than B0's total fruit-fall mass, for the years of 2004-2005, 05-06, 06-07, and 07-08, respectively. In relation to B4, B2 production for the four previous years was: 87%, 84%, 92%, and 73%, for the years of 2004-2005, 05-06, 06-07, and 07-08, respectively.

Relationship between Density, BA, and Fruit-fall Mass

The mass of fruits trapped increased with tree and liana density and BA in trap-centered plots ($r=0.27$, $p<0.001$ mass vs density, $r=0.24$, $p<0.001$ mass vs BA, Figures A-1 and A-2 in Appendix). The linear relationships between these variables were weak as attested by their correlation (Table A-1 and A-2 in Appendix). In addition, the correlation between density and fruit-fall mass and BA and fruit-fall mass varied with treatments and years. Some years the correlation was not significant while in others the correlations among variables were stronger.

Relationship between Distance from the Edge and Fruit-fall Mass

Fruit fall mass in all treatments and years increased from the edge to the interior of the treatment plots ($r=0.19$, $p<0.001$, Figure A-3). This relationship was observed both with all data pooled (Figure A-3.A) and when grouped by year and treatment (Figure A-3.B). Nevertheless, the correlation coefficients varied substantially by year and treatment (Table A-3).

Statistical Models of Fruit-fall Mass Patterns

The global model (the statistical model that encompassed all other models tested) for fruit-fall mass ranked 36th among the 45 models tested, its high AIC, AICc, and low weight indicated that it was not an appropriate model to describe fruit-fall mass.

Wald tests revealed that several terms in the global model were significant ($p < 0.05$; including year, treatment, density, distance, year x density, year x distance, treatment x distance, and the triple-way interaction year x treatment x distance; Table 4-4). The most parsimonious model contained the following terms: year, treatment, distance, density, year x density, year x distance, treatment x distance. In contrast with to the global model, all terms in the selected model were significant ($p < 0.05$, Table 4-5)

The top ranked model had an AIC of 3803.2, AICc = 3805.2 (Figure A-8 for model diagnostics), which indicates that the model has high explanatory power for fruit-fall mass. The fixed effects of the model selected to best represent fruit-fall mass revealed that fruit-fall mass was significantly higher in B4 at larger distances from the forest edge from B0, that is distance and the treatment B4 interacted significantly showing that on average fruit-fall mass increased with distance. Plot B2 and B0 did not show this tendency and fruit-fall mass did not differ among these two treatments (Table 4-6, Figure 4-4). Fruit-fall mass fluctuated among years, consistently showing less fruit-mass per trap after 2004-2005 (Table 4-6). Fruit-fall mass per trap in the burned plots did not differed from the control. Fruit-fall mass increased with higher tree and liana densities. The interaction between density and year was significant for 2008-2009 and marginally significant for 2006-2007; fruit-fall mass tended to be higher per unit density in trap-centered plots in those years when compared to that of 2004-2005 (Figure 4-5). In addition, areas with higher density showed much higher fruit-mass in traps (Figure 4-5). Distance and year significantly interacted in 2005-2006 and 2008-2009; during these years fruit-fall mass was lower at larger distances from the forest edge. In addition, over

all years, there appears to be no statistical difference between fruit-fall mass at the forest edge and up to a distance of 100m (Figure 4-6).

The results statistical analyses of fruit-fall mass are not in agreement with those revealed by descriptive analyses. Fruit-fall mass was shown to be higher in B4 at further distances into the forest by the statistical model. Treatments B2 and B0 did not differ among themselves.

Table 4-1. Summary of fruit-fall mass (g) grouped by year and treatment. Number in parenthesis following mean is the standard error.

Year	2004_2005		2005_2006		2006_2007		2007_2008		2008_2009		total
Treatment	total	Mean	Total	mean	total	mean	total	mean	total	mean	
B0	1438.2	16.0(37.8)	247.1	2.7(5.9)	1053.7	11.7(20.9)	558.1	6.2(11.3)	1854.2	20.6(36.0)	5151.4
B2	2387.2	29.5(61.1)	322.7	4.0(7.8)	1375.0	17.0(30.3)	631.1	7.8(17.6)	795.1	9.8(18.0)	5511.1
B4	2737.2	33.8(80.0)	383.0	4.7(9.6)	1493.9	18.4(32.6)	857.4	10.6(19.0)	1865.6	23.0(43.3)	7337.0
yearly total	6562.6		952.7		3922.6		2046.6		4514.9		17999.4

Table 4-2. Number of traps where fruits were found (in parenthesis percent total traps in treatment) and the area sampled (m², each trap is 0.5 m²).

Year	2004_2005		2005_2006		2006_2007		2007_2008		2008_2009	
Treatment	N. Traps	Area	N. Traps	Area	N. Traps	Area	N. Traps	Area	N. Traps	Area
B0	87(97)	43.5	84(93)	42	87(97)	43.5	89(99)	44.5	87(97)	43.5
B2	81(100)	40.5	71(88)	35.5	77(95)	38.5	71(88)	35.5	67(83)	33.5
B4	81(100)	40.5	72(89)	36	79(97)	39.5	78(96)	39	76(93)	38
Total	249(99)	124.5	227(90)	113.5	243(96)	121.5	238(94)	119	230(91)	115

Table 4-3. Total fruit-fall mass per year and treatment of the 10 most productive species in terms of mass (g) and percentage of the total production per treatment and year.

Year	2004_2005		2005_2006		2006_2007		2007_2008		2008_2009		Total	
Treatment	mass	% total	mass	% total	mass	% total	mass	% total	mass	% total	mass	% total
B0	731.79	50.88	174.87	70.77	891.51	84.61	347.09	62.19	1599.98	86.29	3745.24	72.70
B2	563.81	23.62	180.10	55.82	1022.97	74.40	444.72	70.47	534.89	67.27	2746.49	49.84
B4	1024.93	37.44	278.26	72.66	1127.05	75.44	587.67	68.54	1524.99	81.74	4542.90	61.92
Total	2320.54	35.36	633.23	66.47	3041.53	77.54	1379.48	67.40	3659.86	81.06	11034.64	61.31

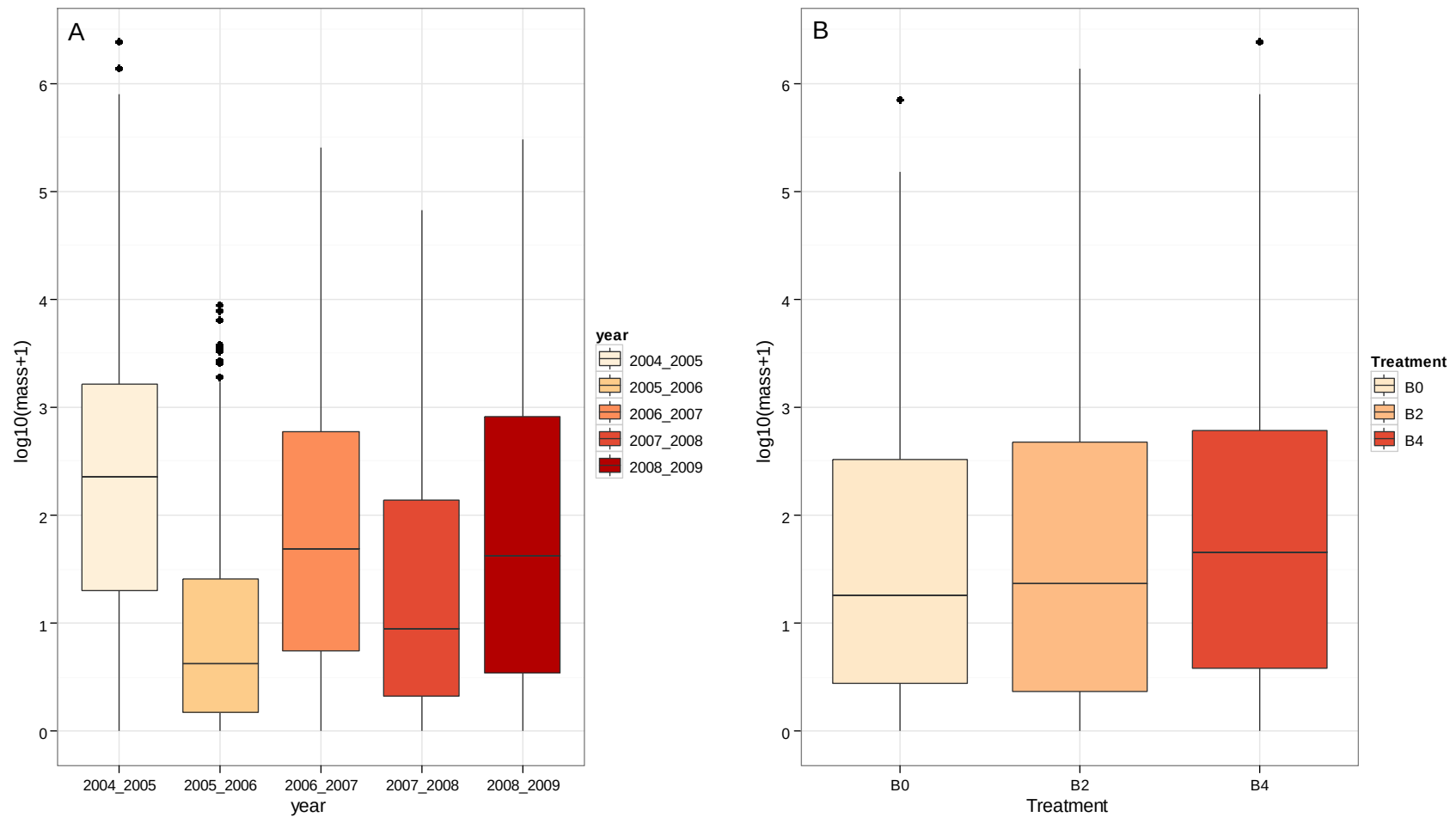


Figure 4-1. Boxplots of fruit-fall mass. A) Yearly total fruit-fall mass ($\log_{10}(\text{mass}+1)$) per trap across treatments. B) Fruit-fall mass per trap per treatment across all years of the study. The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles $\pm$ 1.5 interquartile range, and “♦” are outliers.

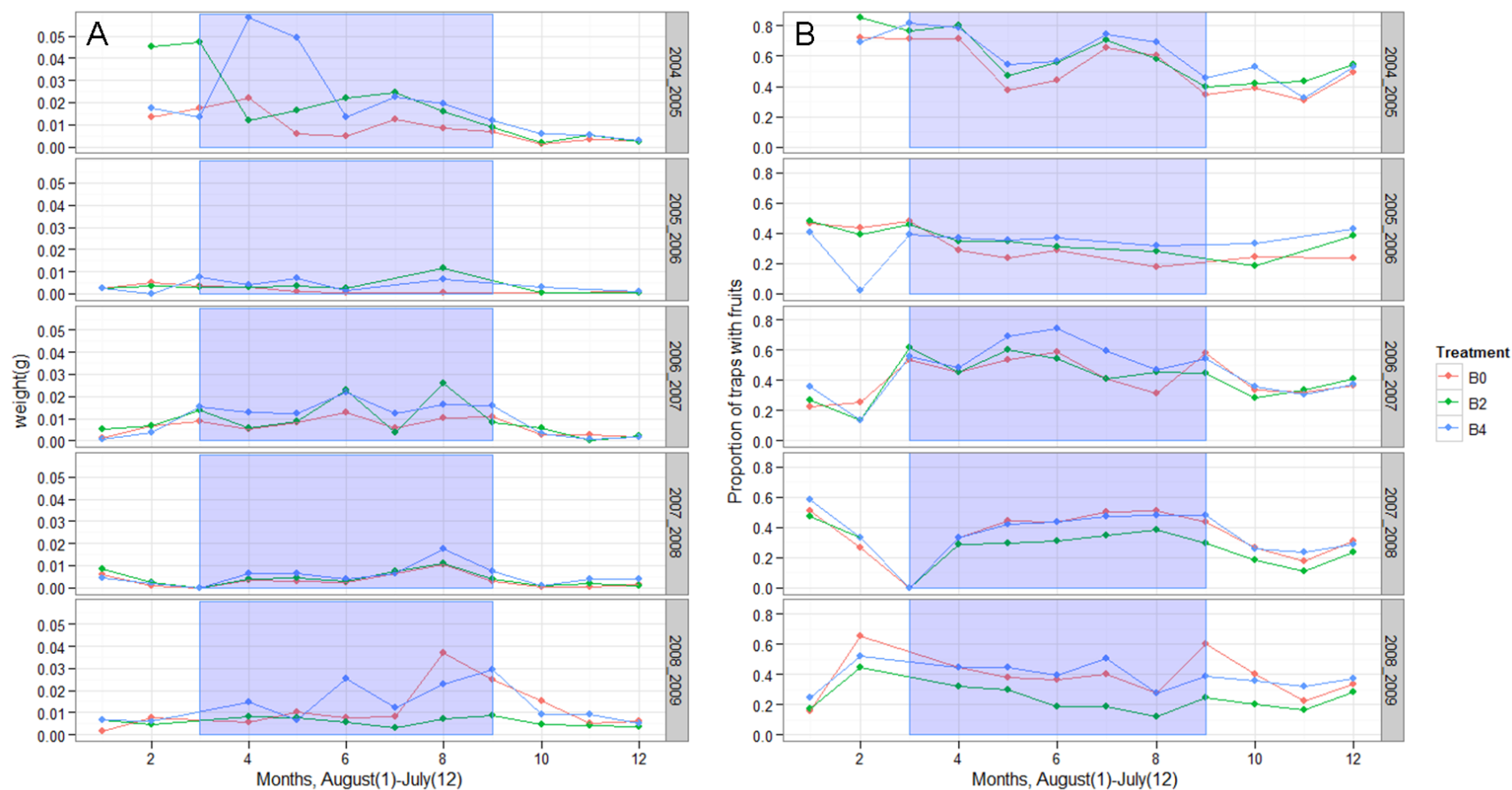


Figure 4-2. Fruit-fall monthly trends across the five years of the experiment. A) Mean monthly fruit-fall mass (g) per treatment and year. B) Proportion of traps containing fruits per month, year, and treatment. Years start on August (1) and end in July (12), shaded area represents months of the rain season.

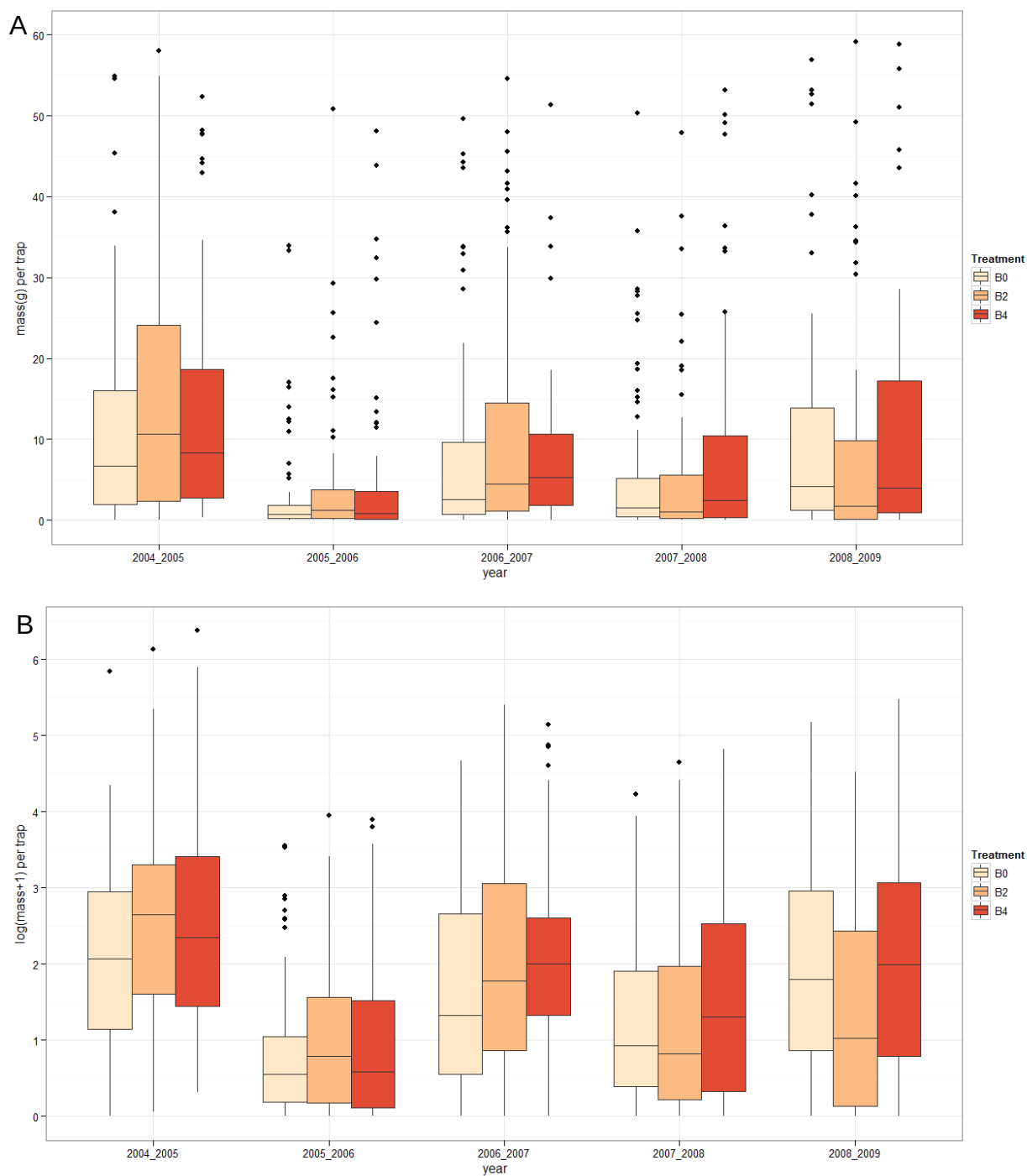


Figure 4-3. Boxplots of fruit-fall mass by treatment and year. A) Untransformed mass (g), with extreme values omitted; B) Log (log10(mass+1)) fruit-fall mass per trap by treatment. The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles +/- 1.5 interquartile range, and “♦” are outliers.

Table 4-4. Wald test statistics for terms in Global model of fruit-fall mass.

	numDF	denDF	F-value	p-value
(Intercept)	1	969	906.8693	<0.001
Year	4	969	96.973	<0.001
Distance	1	246	28.7027	<0.001
Density	1	969	51.7514	<0.001
Treatment	2	246	3.6243	0.0281
year:Distance	4	969	3.2794	0.0111
year:Density	4	969	5.0251	0.0005
Distance:Treatment	2	246	4.114	0.0175
Density:Treatment	2	969	0.8211	0.4402
year:Treatment	8	969	1.2841	0.2479
year:Density:Treatment	8	969	1.0771	0.3767
year:Distance:Treatment	8	969	2.2143	0.0244

Table 4-5. Wald test statistics for selected fruit-fall mass model.

	numDF	denDF	F-value	p-value
(Intercept)	1	995	915.4195	<0.001
Year	4	995	97.1084	<0.001
Distance	1	246	28.9341	<0.001
Density	1	995	50.558	<0.001
Treatment	2	246	3.6354	0.028
year:Distance	4	995	3.2173	0.012
year:Density	4	995	4.8735	<0.001
Distance:Treatment	2	246	4.1237	0.017

Table 4-6. Summary of fixed effects in fruit-fall mass model.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	1.4262392	0.237728	995	5.999461	0.000
2005-2006	-1.189299	0.247012	995	-4.81474	0.000
2006-2007	-0.749551	0.265458	995	-2.82361	0.005
2007-2008	-0.999954	0.233389	995	-4.28449	0.000
2008-2009	-0.579747	0.252856	995	-2.2928	0.022
Distance	0.0005206	0.000417	246	1.247855	0.213
Density	0.0245334	0.008719	995	2.813866	0.005
B2	0.2400206	0.147167	246	1.630941	0.104
B4	0.0653731	0.144196	246	0.453362	0.651
2005-2006 x Distance	-0.000856	0.000366	995	-2.33828	0.020
2006-2007 x Distance	-0.000711	0.000412	995	-1.7244	0.085
2007-2008 x Distance	-0.000438	0.000395	995	-1.10956	0.268
2008-2009 x Distance	-0.001631	0.00046	995	-3.54282	0.000
2005-2006 x Density	-0.001535	0.009828	995	-0.15613	0.876
2006-2007 x Density	0.0208066	0.010983	995	1.894461	0.059
2007-2008 x Density	0.0176516	0.010409	995	1.695724	0.090
2008-2009 x Density	0.0380271	0.011753	995	3.235652	0.001
Distance x B2	0.0003181	0.000459	246	0.69281	0.489
Distance x B4	0.0012745	0.000457	246	2.787067	0.006

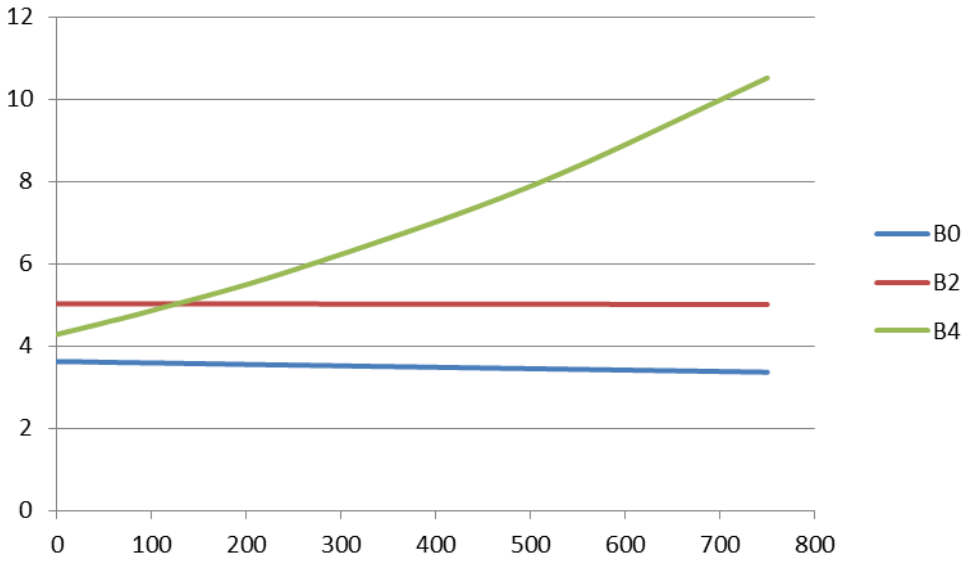


Figure 4-4. Least square means for effects of distance from the forest edge x treatment on fruit-fall mass (g, back transformed values). All other effects in the model are at their average values.

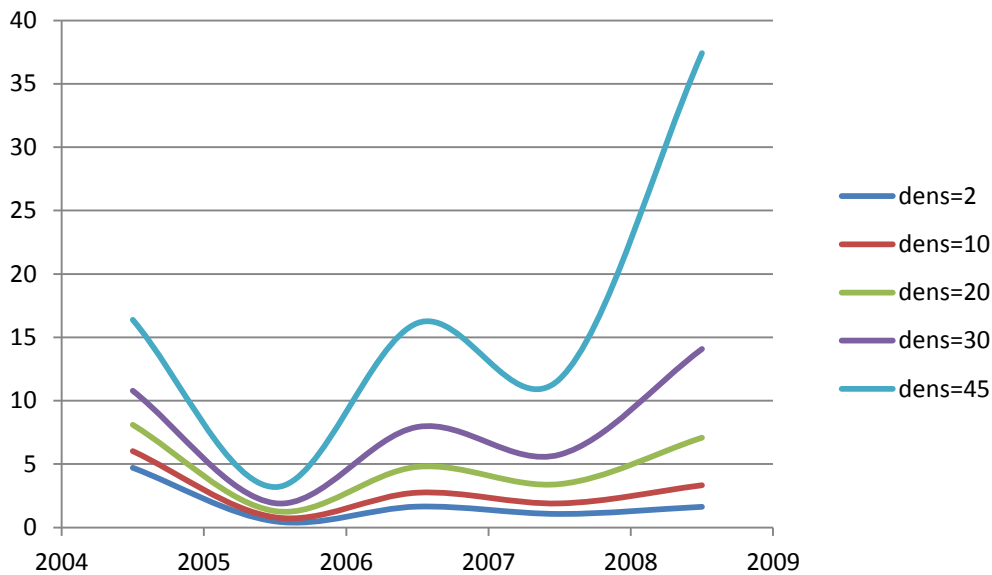


Figure 4-5. Least square means for effects of tree and liana density ("dens") x year on fruit-fall mass (g, back transformed values). All other effects in the model are at their average values.

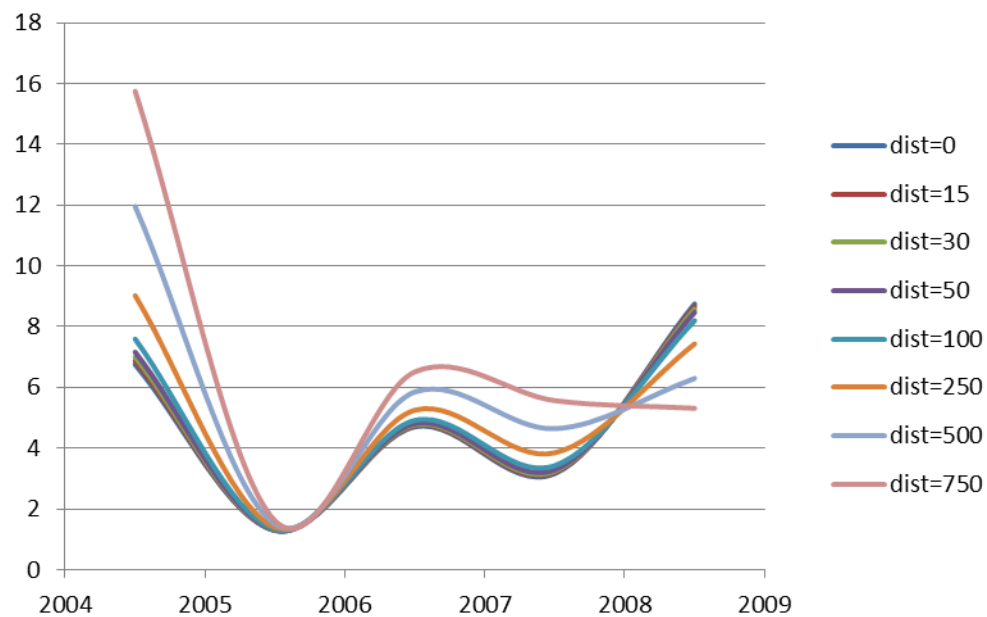


Figure 4-6. Least square means for effects of distance from the forest edge (“dist”) x year on fruit-fall mass (g, back transformed values). All other effects in the model are at their average values.

CHAPTER 5 NUMBER OF SPECIES REPRODUCING

Number of Species Reproducing – Description and Qualitative Analysis

Fruits or seeds of 80 plant species were found in the traps: 73 trees and 7 lianas representing 82% of the total number of trees and lianas species found in the floristic inventory (97). Most species trapped are animal dispersed (70.0%, 56 species), 13.7% (11 species) are anemochoric, and 2.5% (2 species) are autochoric (fruits that explode releasing seeds, found in several species in the Euphorbiaceae), 13.7% (11) species had undetermined dispersal mechanisms. Furthermore the proportion of the fruit-fall mass in different dispersal modes fluctuated yearly but was not affected by the burn treatments (Table 5-1).

The numbers of species found per trap did not appear to differ among treatments (Figure 5-1.A) with medians of 3 species in B0 and B2, and 4 in B4 with years pooled. On an annual basis (with treatments pooled), the number of species found per trap in 2004-2005 (median=6), 2006-2007 was the second highest (median=4), and the other years all had median=3 (Figure 5-1.B).

The number of species in fruit-fall varied monthly and yearly but did not show any divergence among treatments with time. Unlike fruit-fall mass, the number of species in fruit was not clearly seasonal (Figure 5-2.A).

Relationship between Number of Species and Distance, Density, BA, and Diversity

The number of species per trap with all treatments and years pooled increased with Distance from the forest edge ($r = 0.25$, $p < 0.001$, Figure A-4). This relationship was also observed with data grouped by year and treatment, though it remained weak

(Figure A-4.B and Table A-4). The number of species per trap as a function of distance varied by year and treatment and at times yielded high correlations.

The number of species falling into individual traps increased with tree and liana densities ($r = 0.38$, $p < 0.001$) and BA ($r = 0.31$, $p < 0.01$) in trap-centered plots (Figure A-5 and A-6, respectively). When the relationship between number of species and tree and liana density were grouped by treatment and year, the correlation varied substantially, again, with some years yielding high correlations (Table A-5). The correlation of tree and liana density with number of species in B2 tended to increase over the years. The correlation between number of species and BA also varied by year but was usually lower than the correlation between tree and liana density and number of species (Table A-6). Increasing diversity per trap-centered plot also had an increasing effect on the number of species in fruit-fall ($r=0.26$, $p < 0.001$ Figure A-7).

Quantitative Analysis of Number of Species in Fruit-fall

Model selection procedures arrived at the following model: year, treatment, distance, density, year x density, year x distance, treatment x density, and treatment x distance (Table 5-2). All terms were significant at $p < 0.05$ except for treatment x distance ($p=0.099$, Wald test). This model had AIC = 5248.5, AICc = 5249.6, and weight = 0.164. The next model in the analysis contained the same terms except for treatment x distance interaction, and all terms were significant ($p < 0.05$; Table 5-3). This model was not considered statistically different from the model with lowest AIC, AICc, and highest weight ($p=0.09$). Thus by the principle of parsimony we selected the second model given that there are no differences and the second model contains $k=23$ parameters while the first contains $k=25$. For this model, AIC = 5249.3, AICc = 5250.2, and weight = 0.1182.

The model selected for further inquiry of the data had several interaction terms: treatment x density, year x density, and year x distance. The treatment x density interaction indicated that treatment B2 have more species present in its traps at high tree and liana densities than the control. Treatments B2 and B4 did not have different number of species at any density levels. In addition B4 and B0 did not differ in this regards (Figure 5-3). The number of species tended to be higher at high levels of tree and liana density for all years with the year of 2004-2005 always having a higher number of species and 2005-2006 consistently having the lowest number of species (Figure 5-4). The year x distance interaction indicated that for all years except 2008-2009 the number of species in fruit-fall tended to increase with increasing distance from the edge with a steeper increase beyond 100 m from the forest-agriculture edge (Figure 5-5). For the year 2008-2009 this interaction indicated that differently from the other years, the number of species tended to decline with increasing distance from the forest edge. Furthermore the year 2004-2005 had the highest number of species found and 2005-2006 the lowest.

Comparing the qualitative and quantitative analyses of the number of species in fruit-fall we observed that some of the conclusions differ. The number of species did fluctuate yearly and this was revealed by both analyses. In addition there was a tendency for the number of species to increase with both increasing distance from the edge and the density of trees and lianas surrounding the traps. The quantitative analysis, however, indicated that the number of species in fruit-fall in treatment B2 was higher at high tree and liana densities when compared with the control. This result

differs from the pure interpretation of graphs and tables, which, on the contrary, indicates that B2 had less species falling in its traps than the B0.

Table 5-1. Summary of fruit mass (g) by dispersal mechanism and percent of total mass by dispersal mechanism per treatment and year.

Year	Treatment	B0		B2		B4	
	Dispersal	Total mass	% of total	Total mass	% of total	Total mass	% of total
2004-2005	auto	5.33	0.37	3.36	0.14	12.21	0.45
	anemo	201.23	13.99	585.25	24.52	410.22	14.99
	zoo	1219.23	84.77	1783.39	74.71	2282.12	83.37
	undet	12.45	0.87	15.21	0.64	32.63	1.19
2005-2006	auto	9.59	3.88	2.93	0.91	2.09	0.55
	anemo	1.83	0.74	4.33	1.34	0.05	0.01
	zoo	234.10	94.74	314.32	97.42	378.74	98.90
	undet	1.57	0.64	1.07	0.33	2.08	0.54
2006-2007	auto	8.16	0.77	3.31	0.24	1.92	0.13
	anemo	8.49	0.81	25.25	1.84	27.40	1.83
	zoo	1032.06	97.95	1339.91	97.45	1457.98	97.59
	undet	4.97	0.47	6.54	0.48	6.61	0.44
2007-2008	auto	13.05	2.34	12.56	1.99	8.77	1.02
	anemo	38.39	6.88	111.07	17.60	69.11	8.06
	zoo	486.72	87.21	506.30	80.22	753.80	87.92
	undet	19.96	3.58	1.18	0.19	25.70	3.00
2008-2009	auto	33.11	1.79	17.58	2.21	5.42	0.29
	anemo	189.25	10.21	122.50	15.41	108.83	5.83
	zoo	1561.64	84.22	651.33	81.92	1750.41	93.83
	undet	70.22	3.79	3.70	0.47	0.90	0.05

(Dispersal mechanism: auto=autochoric, anemo=anemochoric, zoo=zoochoric, and undet=undetermined.)

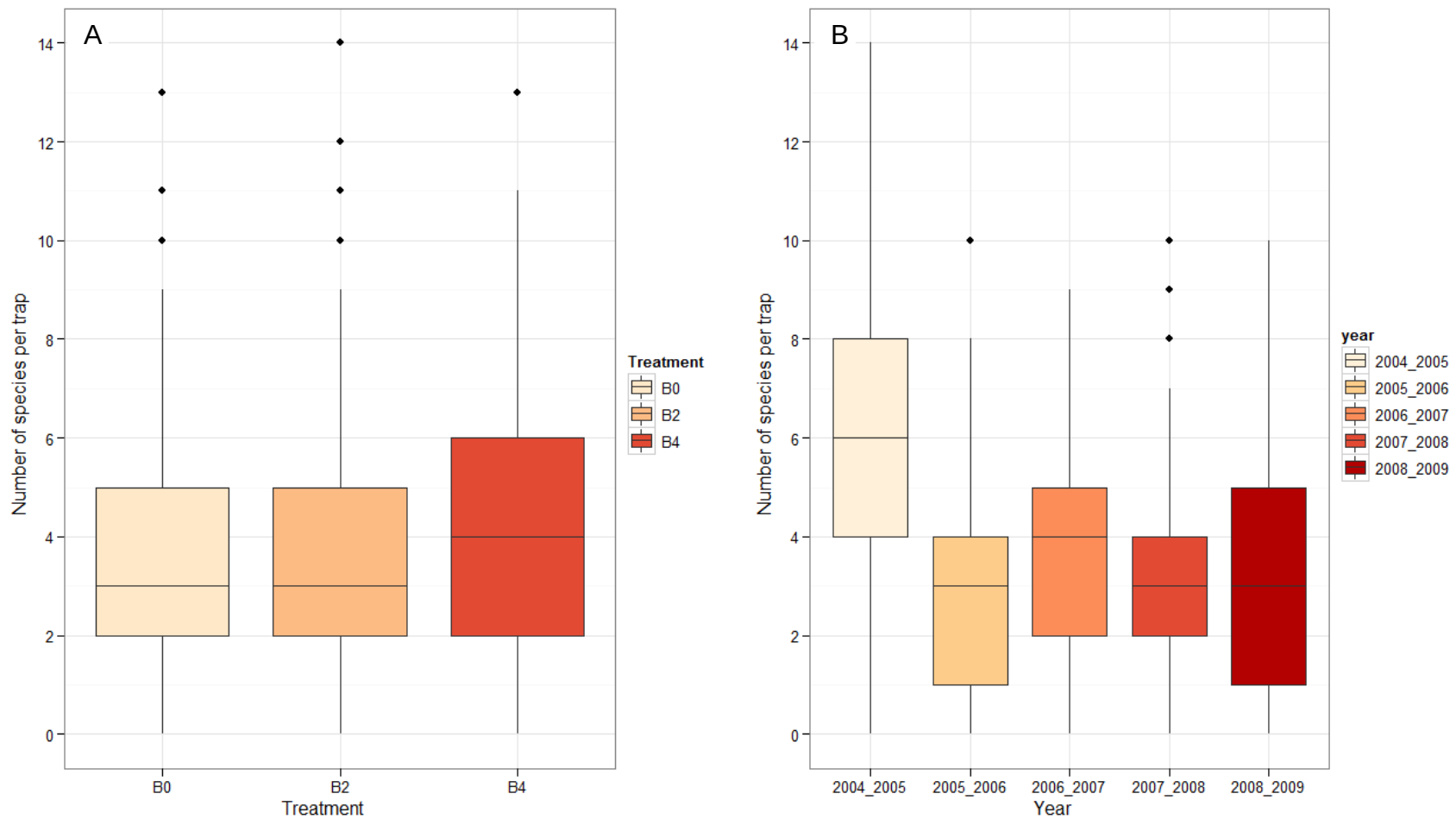


Figure 5-1. Boxplots of number of species in fruit traps. A) Number of species per trap per treatment, all years pooled. B) Yearly number of species per trap, treatments pooled. The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles +/- 1.5 interquartile range, and “♦” are outliers.

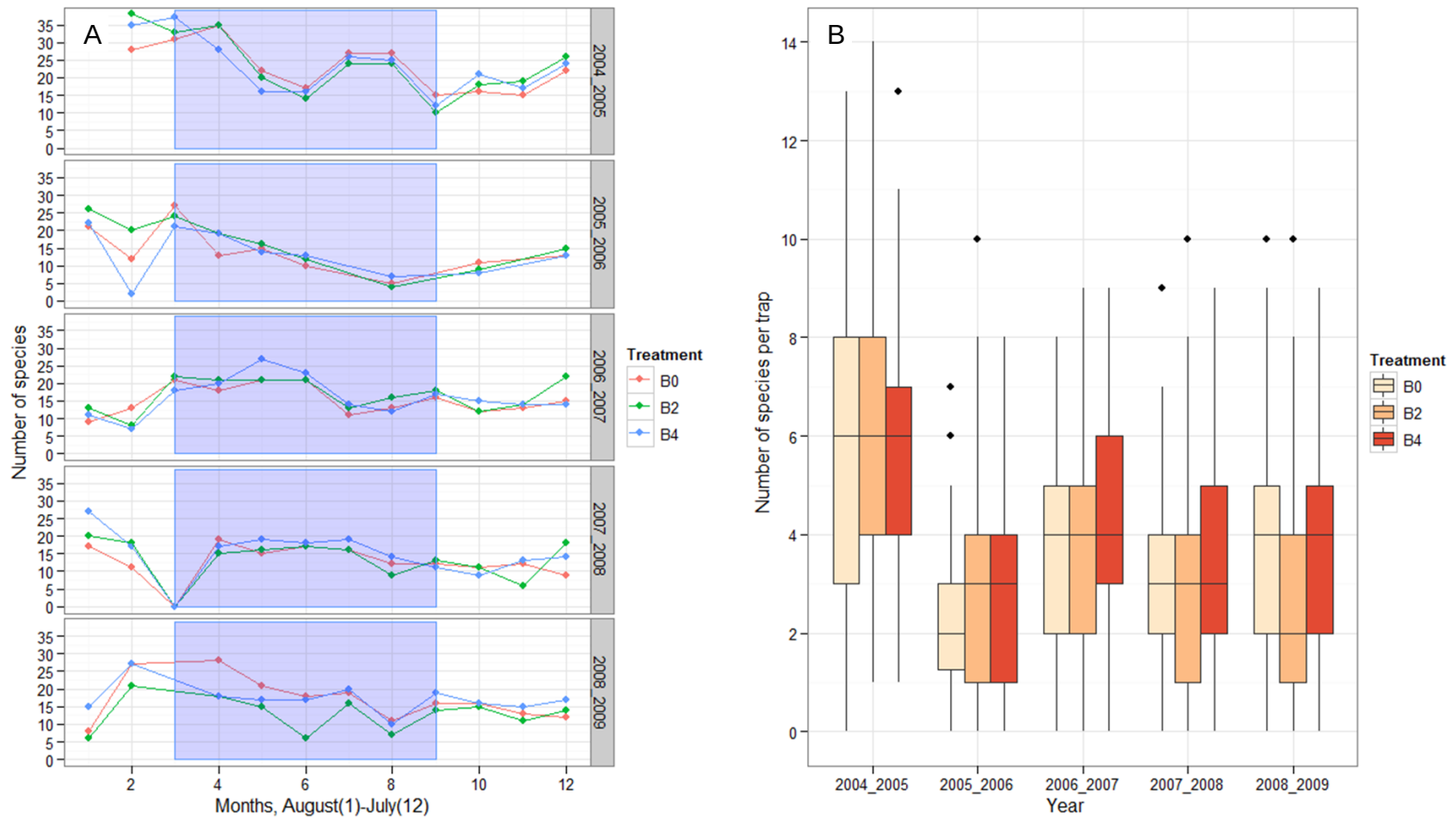


Figure 5-2. Number of species per month, treatment, and year. A) Total monthly number of species per treatment during the five year study period (shaded area indicates rain season). B) Boxplots of the number of species found per trap per year and treatment. The boxplot represents the 25th, 50th, and 75th percentile, whiskers are the first and third quartiles ± 1.5 interquartile range, and “♦” are outliers.

Table 5-2. Wald tests for terms in model of lowest AIC for number of species in fruit-fall.

	numDF	denDF	F-value	p-value
(Intercept)	1	994	2407.295	<0.0001
Treatment	2	994	3.7494	0.0239
Density	1	994	181.5677	<0.0001
Distance	1	994	9.3542	0.0023
year	4	994	100.5062	<0.0001
Treatment x Density	2	994	4.4186	0.0123
Treatment x Distance	2	246	2.339	0.0986
Density:year	4	994	2.6209	0.0336
Distance:year	4	994	6.3576	<0.0001

Table 5-3. Wald test for terms in the final, most parsimonious, statistical model of number of species in fruit-fall.

	numDF	denDF	F-value	p-value
(Intercept)	1	994	2383.22	<0.0001
Treatment	2	994	3.6573	0.0261
Density	1	994	180.29	<0.0001
Distance	1	994	12.7393	0.0004
Year	4	994	99.7178	<0.0001
Treatment x Density	2	994	4.3789	0.0128
Density:year	4	994	2.6299	0.0331
Distance:year	4	994	6.3399	<0.0001

Table 5-4. Summary for the model selected to further analysis of the number of species in fruit-fall.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.919191	0.481291	994	8.143086	0
TreatmentB2	-0.84614	0.410483	994	-2.06132	0.0395
TreatmentB4	-0.16809	0.444622	994	-0.37806	0.7055
Density	0.049871	0.019416	994	2.56856	0.0104
Distance	0.002193	0.000581	994	3.774992	0.0002
2005-2006	-2.12446	0.440284	994	-4.82519	0
2006-2007	-0.91692	0.447371	994	-2.04956	0.0407
2007-2008	-1.60958	0.434099	994	-3.70787	0.0002
2008-2009	-1.50358	0.449903	994	-3.342	0.0009
TreatmentB2 x Density	0.044786	0.017191	994	2.60518	0.0093
TreatmentB4 x Density	0.020641	0.018349	994	1.124935	0.2609
Density x 2005-2006	-0.02777	0.01764	994	-1.57417	0.1158
Density x 2006-2007	-0.02694	0.018446	994	-1.46036	0.1445
Density x 2007-2008	-0.01844	0.019521	994	-0.94471	0.345
Density x 2008-2009	0.024084	0.020545	994	1.172273	0.2414
Distance x 2005-2006	-0.00115	0.000654	994	-1.7528	0.0799
Distance x 2006-2007	-0.00106	0.000683	994	-1.54505	0.1227
Distance x 2007-2008	0.000511	0.000741	994	0.689233	0.4908
Distance x 2008-2009	-0.00277	0.00078	994	-3.55421	0.0004

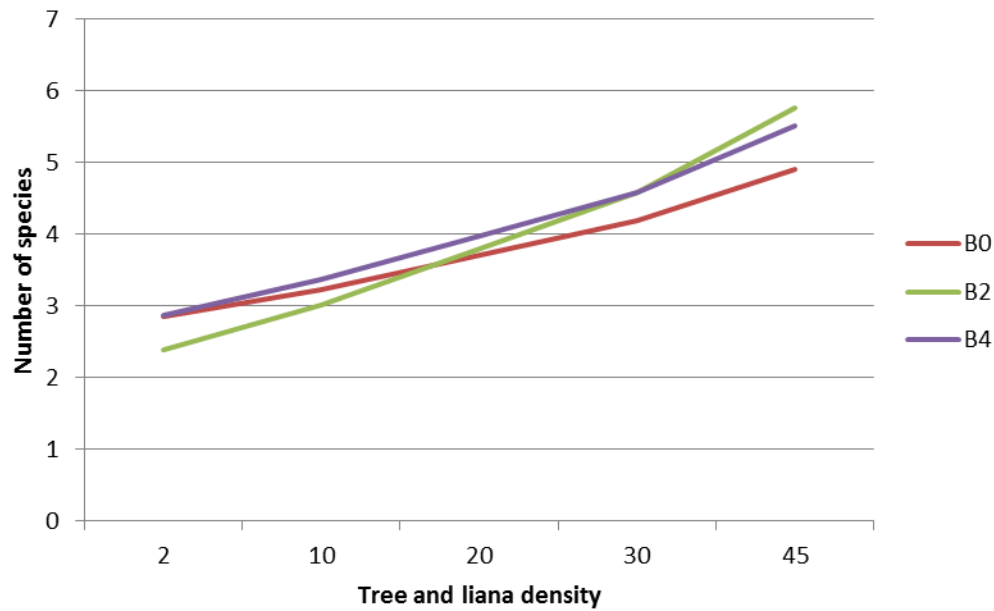


Figure 5-3. Least square means values for the number of species in fruit-fall treatment x density interaction. All other effects in the model are at their average values.

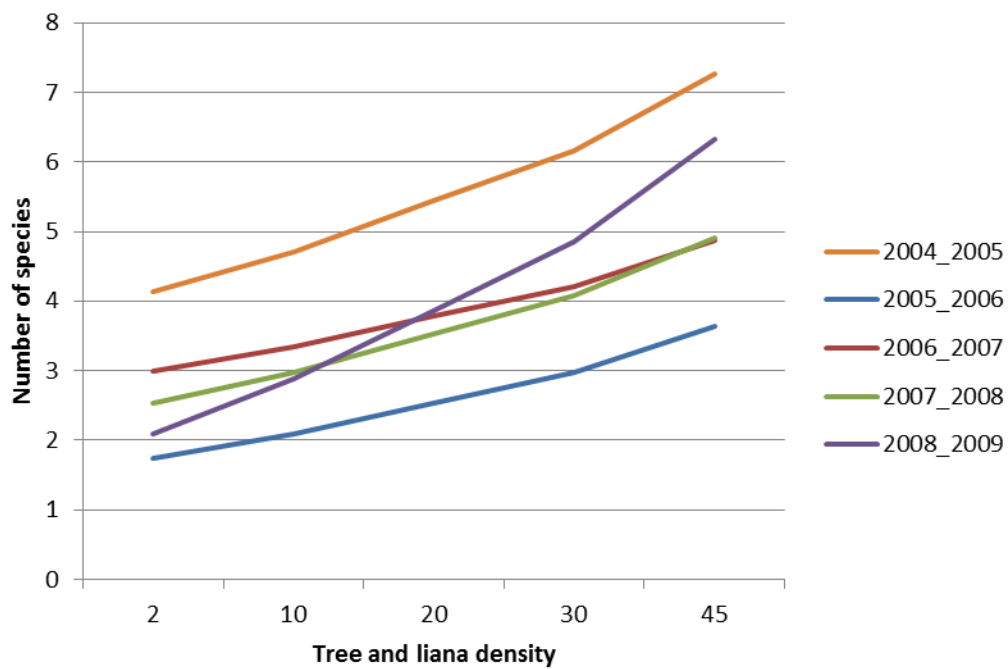


Figure 5-4. Least square means values for the number of species in fruit-fall year x density interaction. All other effects in the model are at their average values.

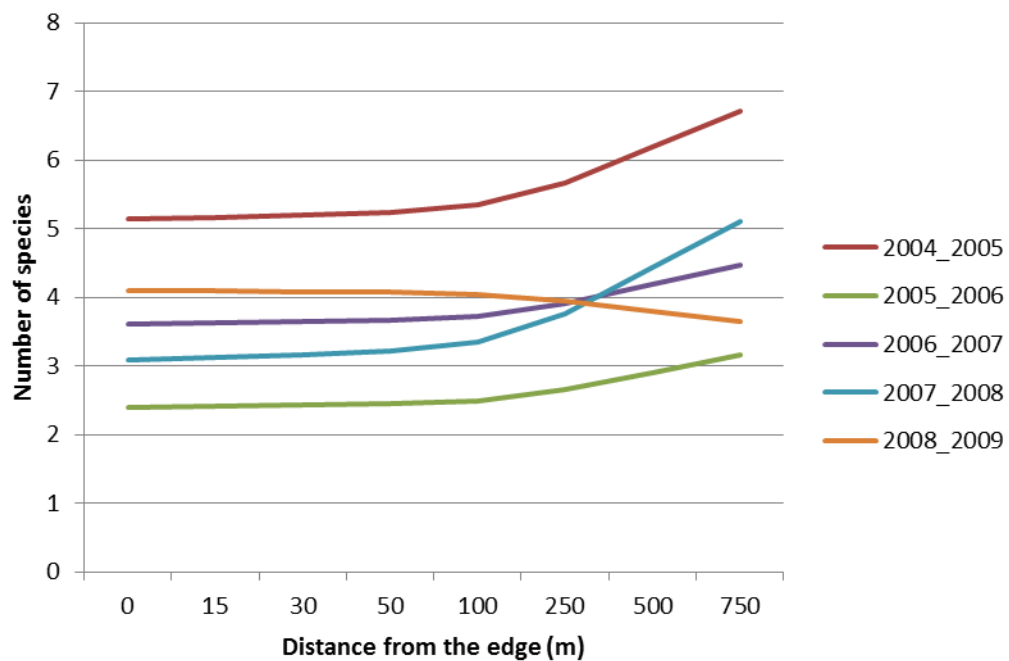


Figure 5-5. Least square means values for the number of species in fruit-fall year x distance interaction. All other effects in the model are at their average values.

CHAPTER 6 DISCUSSION

Fire and Edge Effects on Forest Structure

Burning caused reductions in tree and liana density, BA, and diversity. The two fire treatments differed in their impacts, with generally larger decrease in all variables in B2 than in B4 by the last year of this study. A more pronounced decrease was observed after the 2007 experimental fire in both B2 and B4. This effect might be attributable to the fact that 2007 was a dry year (Paulo Brando pers. comm.). Droughts increase the risk of understory fires in the Amazon (Nepstad et al. 2004), but also increase fire intensity and severity. Thus the high severity of the 2007 fire may be in part due to the dryness of that year.

The observed reductions in density and BA after repeated burns are in accord with other studies reporting on the effects of recurring fires. Balch et al. (2008) noted that short fire return intervals (FRI; as in B4, ~1 year), are associated with decreased area burned, lower flame heights, and due to a lack of fuels. The short FRI in B4 appears to have buffered trees and lianas from fire-induced mortality, which resulted in less fire impact on tree and liana density, BA, and diversity than in B2. In contrast, less frequent fires in B2 allowed litter-fall and debris of fire-killed trees to accumulate between the first and second fire. Fuel accumulation together with dry weather converged to cause a more dramatic reduction in density, BA, and diversity in B2 after the 2007 fire.

Fire and proximity to the forest-agriculture edge interacted to influence mortality. In other words, there was an effect of distance from edge on density, BA, and diversity that was influenced by fire. Burning, particularly in B2, caused decreases in the intercepts and increases in slopes of the relationship between density, BA, and diversity

with distance from the edge after repeated fires. The decreases in intercepts indicate that there was an overall reduction in the average values of these variables due to fire at the forest-agriculture edge. Increase in slopes after repeated burns indicate that there was there was a differential reduction in density, BA, and diversity closer to the edge than further into the treatment plots.

Fire Treatments Did Affect Fruit-fall Mass but at Long Distance from the Edge

Contrary to our expectations, fire did cause a decline on fruit-fall mass. Rather, as evidenced by our results there was no apparent divergence in fruit-fall mass by year and treatment. Treatment B4 actually had a higher fruit mass at larger distances from the forest edge than the control treatment and B2 and B0 did not differ statistically. It is worth considering that when the analysis was run with only the interior traps (i.e. those at least 100 m from any edge) the treatment x distance interaction was significant and revealed that B4 had a higher fruit mass falling in tis traps than B0. Additionally when the variable distance was removed from the statistical analysis treatment B4 did present higher fruit mass than B0 while B0 and B2 did not differ in this regards. This emerged despite considerable decreases in tree and liana densities and basal areas, which would be expected to result in fruit production declines (Barlow and Peres 2006a, b). Even though after the 2007 fire tree and liana density and BA decreased markedly and to comparable levels as those reported by Barlow and Peres (2006b), still there were no decreases in fruit-fall mass during two years after that fire (2008-2009). Barlow and Peres (2006b) observed that fewer trees were in fruit in burned forests with numbers further decreasing in twice burned forests. If this response held in our forest, then our results are enigmatic.

Greater Influx of Fruits into Burned Plots

One potential explanation for the patterns of fruit-fall mass observed in this study is increased use of burned forest by seed dispersing animals that deliver fruits from outside the burned plots. Few studies have addressed the effects of tropical forest fires on wildlife thus we both draw examples from fire studies as well as from logging studies. Barlow et al. (2002) observed a decline in overall bird species richness and abundance after fires in Amazon forests; in particular this effect was more prominent for habitat specialists, rare, and disturbance-sensitive species. In contrast, these authors observed increases in nectar and seed eaters. Barlow and Peres (2004) studied bird responses one and three years after an understory Amazon fire and reported that substantially more individuals and species were captured three years after the fire. These authors also reported a marked increase in frugivorous birds, which was correlated with the number of small woody stems (dbh<10cm). They also report an increase in abundance of second-growth forest bird species, which they related to the open forest canopy that resulted from burning.

Barlow and Peres (2004) relate their finding in burned forest with those of studies of avifaunal responses in logged forests, concluding that the responses are similar. In another study, Lambert (1992), found significant increases in the abundance of nectarivores-insectivore-frugivore birds in selectively logged forests when compared to unlogged forest in Borneo. In Guiana Thiollay (1997), found overall canopy bird abundance to be unaltered in logged forest, with increases in species associated with forest edges, dense second growth, and large gaps. These studies suggest increased use of burned and logged forests by frugivorous birds, which support the idea that birds came into the burned plots from undisturbed areas and delivered seeds. Conversely, if

frugivorous bird abundance increases following burning or logging it likely does so because of shifts in availability of resources utilized by this foraging guild. Increased frugivore abundance may be a reflection of increased fruit availability in disturbed forests. Barlow and Peres (2004) for example related the number of fruit and nectar eating birds to the number of small woody stems and heliconia stems, both of which produce resources for these foraging guilds. In addition Barlow and Peres (2006b) report that smaller trees 10-20 and 30-40 cm dbh bore fruit more often than expected in burned forests.

Increased Availability of Resources in Burned Forests Leads to Increased Reproductive Output Survivors

Fire, like other disturbances, influences the availability of resources, by opening space that otherwise would be occupied (Bond and Wilgen 1996). Surviving individuals enjoy greater resource availability that can be allocated to reproduction. Few studies have dealt with the effects of disturbances on tropical forest tree and liana reproductive output, in particular in relation to community-wide responses. The sheer number of species is daunting (our study found 80 species in fruit-fall traps from a total of 97 tree and liana species). The few studies that tackled the response of one or a few species to disturbance and may provide a starting point to argue in relation to results observed on the present thesis. In addition, we also draw on information from temperate, sub-tropical, and tropical forest management examples.

Logging is comparable to fire insofar as it removes standing biomass (but through a very different selection process). In any case, surviving individuals enjoy increased availability of resources and display what is generally called a “release.” Release cuts

can be both for enhancing growth of remaining trees in a stand as well as to enhance reproductive output (i.e. increase seed production).

In experiments with loblolly pine (*Pinus taeda*) Wenger (1954), found that released individuals consistently produced more cones and markedly increased three years after the treatment. Karlsson (2000) working with Scots pine (*Pinus sylvestris*) in Sweden, reported a similar trend for released trees: more cones were produced by released trees, and he observed a five-fold increase in cone production 4 to 5 years after the release. In a study of three species of oaks in managed forests Barik et al. (1996), reported that in two, *Lithocarpus dealbatus* and *Schima khasiana* acorn production increased with increasing levels of disturbance. The third species, *Quercus griffithii*, did not show increases in acorn numbers but produced heavier seeds in disturbed sites.

In logged Costa Rican montane forests Guariguata and Saenz (2002) estimated acorn production at the stand level. They report that the number of acorns of *Quercus costaricensis* that fell per unit of ground area was highest after the highest cutting level (30% basal area removal). At 20% basal area removal they report that acorn numbers were marginally higher than within un-logged forest stands. These authors attributed their results in part to an increase in the number of trees fruiting earlier than expected based on their size classes.

While these studies show that individual trees increase fruit production after disturbances such as logging, it is not possible to discern whether this effect is scalable to the community-level. In addition, some studies report the opposite pattern. Ghazoul et al. (1998), studying the Dipterocarpaceae *Shorea siamensis*, found that fruit set was lower per tree than in disturbed sites (disturbed sites had 22 trees dbh>10 cm per ha,

undisturbed 205 trees/ha). These authors attributed the decrease in fruit set to the decrease in *S. siamensis* density resulting in increasing distance between individuals. The increased distances between individual trees decreased pollinator visitation, causing bees to remain longer periods foraging on fewer tree individuals and consequently not favoring pollen transfer.

The effects of fire on reproductive output of plants are also reportedly mixed. In fire-prone ecosystems, fire is reported to stimulate flowering in several species (Whelan 1995, p. 87). The mechanism by which fire stimulates flowering is not understood but may be related to increased post-fire resource availability (Whelan 1995). Whelan also suggests that fire damage and pruning might also stimulate flower primordia initiation. Though increased flowering has been reported in burned temperate and sub-tropical forest ecosystems it is not possible to ascertain whether tropical forests are stimulated in a similar manner as no study has specifically dealt with this issue. In neotropical savannas, the effects of fire on tree reproduction are also mixed. Hoffmann (1998) reported that only one out of the six species studied showed marked post-fire increases in fruit production. He concluded that frequent burning had a negative effect on sexual reproduction. Because the only studies of fruiting in burned tropical forests are those of Barlow and Peres (2006a and b), it is not clear what would be reasons for the patterns reported in the present thesis. Barlow and Peres (2004 and 2006b) did observe that smaller stems dbh <10 cm fruited more often in burned than in unburned forests. This observation conforms to the above-mentioned studies in logged forests and may partially account for the lack of differences in fruit-fall mass between treatment B2 and the control and the higher fruit-fall mass in B4 than in B0. In addition to increased

fruiting by small individuals, larger individuals may also increase their fruit production after fires.

If such patterns of fruit-fall mass are a result of increased fruit production by surviving individuals, an interaction between tree density and treatment would be expected but not observed. That said, this study was not designed to assess fruit production by surviving individuals. Chapman et al. (1994) argue that while fruit-fall traps are a suitable method to conduct comparisons of habitats and different study areas, data in fruit-fall traps cannot be equated to fruit production since they measure fruit-fall and not fruit production. Thus, to take the next step and relate fruit-fall mass to changes in density of surrounding individuals might not yield results because the content of traps poorly relates to fruit production by the surrounding trees.

Fire and Edge Did Interact to Influence Fruit-fall

Our results indicate a significant interaction between treatment and distance from agricultural edge for B4. This interaction was expected on the basis of that tree mortality due to fire would be comparatively greater closer to forest edges than further into forest patches. Contrary to our expectations, however, fruit-fall mass was higher further into the treatment plot in B4 than in the control. As mentioned above B2 and B0 did not differ in this regard, neither did B2 and B4. This interaction might have emerged given that the density of trees and lianas tended to increase with increasing distance from the edge and because in B4 the decline in tree and liana density was not very pronounced as in B2. The decline however might have been just enough to cause an increase in production in that treatment. In B2, on the other hand, the observed decrease in tree and liana density might have been too great to cause an increase in fruit-fall mass to levels higher than those of B0. Despite the significance of the interaction it is difficult to

ascertain causation to fire. Since fruit-fall data was only initiated after the fire treatments it is not possible to determine whether the observed was already in place before burning activities began. In addition, following the fact that fire kills more trees in the edge than in the forest interior, we would also expect to observe the distance x treatment interaction for B2. Our results indicate that fire did influence the relationship between the density of trees and lianas and distance from edge on B2, this influence is noted as a decrease in the model intercept with subsequent fires and an increase in regression slopes. The increased regression slopes indicate that a higher proportion of trees and lianas were killed closer to the edge in comparison to areas further into the forest plots. The assumption that fire induced mortality will cause a decrease in fruit-fall mass is not supported rather as observed in this study and corroborated by previous studies reduction in tree density have an opposite effect than that expected.

Fire Did Affect Fruit-fall Species Richness

The number of species in fruit-fall traps was higher in B2 at higher tree and liana densities than in the control. Treatments B4 and B0 did not differ as well as B4 and B2 in this regards. These results were un-expected as the diversity of trees and lianas declined in both fire treatments. In particular both diversity and density of lianas decreased markedly in B2. One explanation to the observed pattern revealed by the statistical analysis is that in B2 fire might have induced earlier fruiting by some species and/or more continuous fruiting by others. The consequences of this would be that in B2 some species would be fruiting while in the other plots the same species would not be. Note that the larger number of species observed does not entail a greater mass of fruits falling into the traps. In the analysis of species richness in fruit-fall if the mass value that

each species contributed was not determinant of them being considered to be considered to be present or not (it was enough to have fruit mass > 0 g to be included).

Implications for Regeneration of Burned Tropical Forests

Assuming that the number of seeds of a given species is related to the mass of its fruits, we can argue that number of seeds reaching the forest floor of the frequently burned treatment (B4) was greater than the control while for the twice burned forest (B2) burned it did not differ from the unburned control. In addition, the number of species did not decline (actually increased in B2) due to fire, which suggests that not only the availability of propagules for regeneration may actually increase or remain unchanged but that the number of species that could potentially regenerate in the post-fire environment remains constant or increases. Based on the findings of (Norden et al. 2007) in French Guiana, the numbers and identities of the seedlings germinating in a forest site are strongly related to variation in seed fall. This relationship suggests (given the assumption that fruit-fall mass is related to seed fall quantities) that burned forest regeneration is not limited by seed availability. It remains to be determined whether fire induced changes in the species composition of the fruit-fall. Changes in species composition of seed fall would affect forest regeneration and future composition of burned forests community. It is also not yet clear how different species respond to post-fire environments; some species may flourish under the new conditions while others languish.

The prospects for increased incidence of forest fires in the Amazon and the positive fire-feedbacks under certain fire return intervals may restrict regeneration in burned tropical forests. Thus even if the potential for forest regeneration, as indicated by seed input, remains unaltered by fire, repeated fires will likely hamper regeneration both

by killing seedlings and damaging seed banks (Kennard et al. 2002). Without protection of burned forests from repeated fires, the prospects for forest to recovery remain low. In addition, repeated burns are likely to lead to a level of fruit tree loss that inevitably will cause fruit-fall levels to decrease in burned forests. In environments where fires are common, vegetative reproduction may be favored over sexual reproduction in ensuring plant survival (Hoffmann 1998).

CHAPTER 7 CONCLUSION

This thesis reports results on the effects of repeated fire on fruit-fall patterns in a transitional forest on the southern edge of the Amazon Basin. Our results indicate that five year after the initiation of the experimental fires fruit-fall patterns were altered by fire, but results were in contrast with our expectations. Fruit-fall mass showed an increase with increasing distance from the edge in treatment B4 and fruit-fall mass did not differ among treatments B2 and B0 (control). The number of species in fruit-fall was greater at higher tree and liana densities in B2.

Our study is the first to address the issue of fruit-fall in burned tropical forest. The temporal and spatial extent of this experiment ensures that the results bear some inferential strength related to the effects of burning on fruit-fall. Our results indicate that regeneration in burned forests might not be limited by a lack of seed input. This realization warrants further studies on the limitations to plant regeneration in burned forests and ways to foster forest recovery.

Finally, although we have shed some light into an important process in the ecology of tropical forest many questions remain unanswered and many more has risen from the results we presented.

APPENDIX A
VARIABLE CORRELATIONS, STATISTICAL MODELS, MODEL SELECTION, AND DIAGNOSTICS

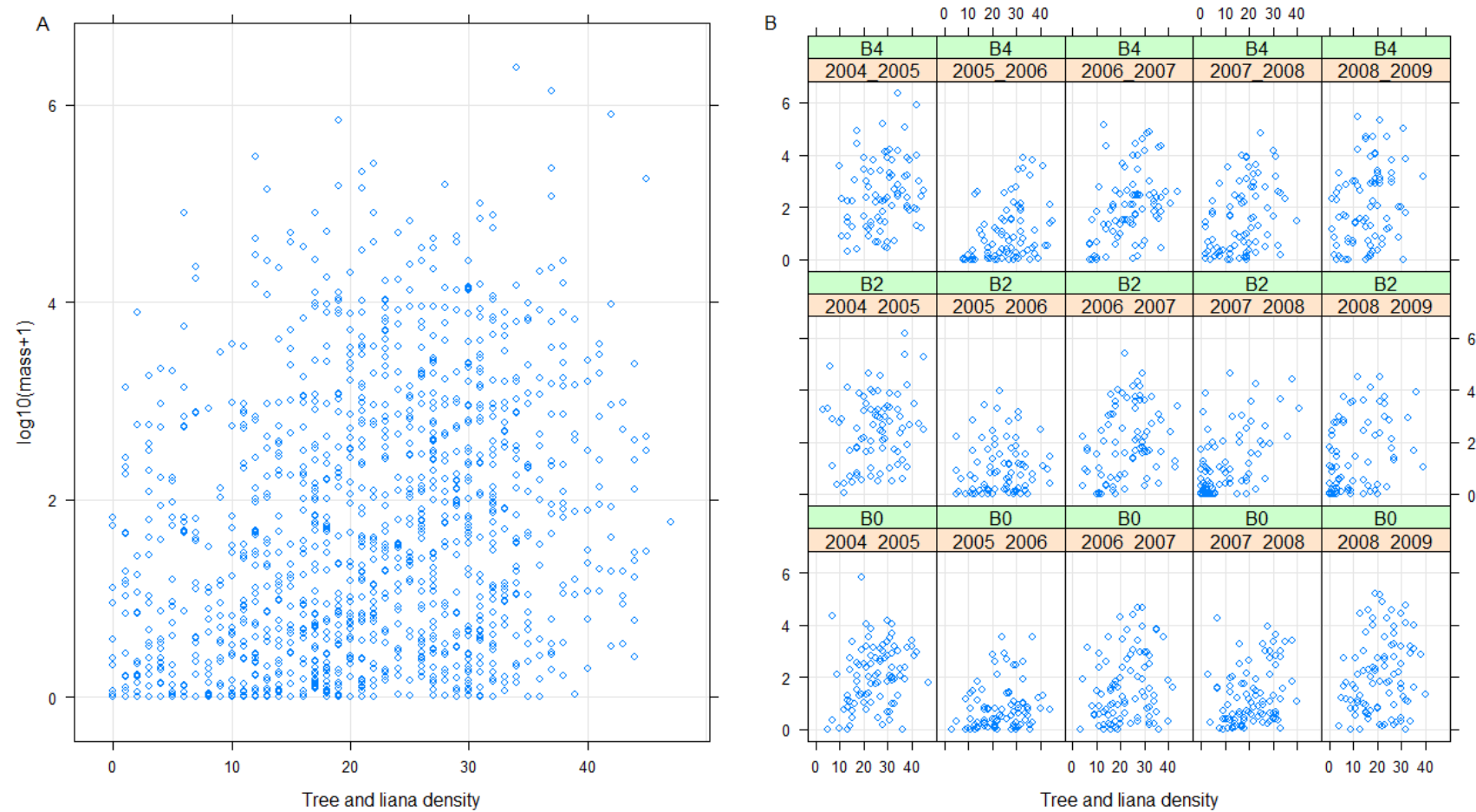


Figure A-1. Distribution of fruit-fall mass ($\log_{10}(\text{mass}+1)$) by tree and liana densities in trap-centered plots. A) All treatments and years pooled ($R = 0.28$, $p < 0.001$; $\rho = 0.3$, $p < 0.001$). B) Grouped by treatment and year.

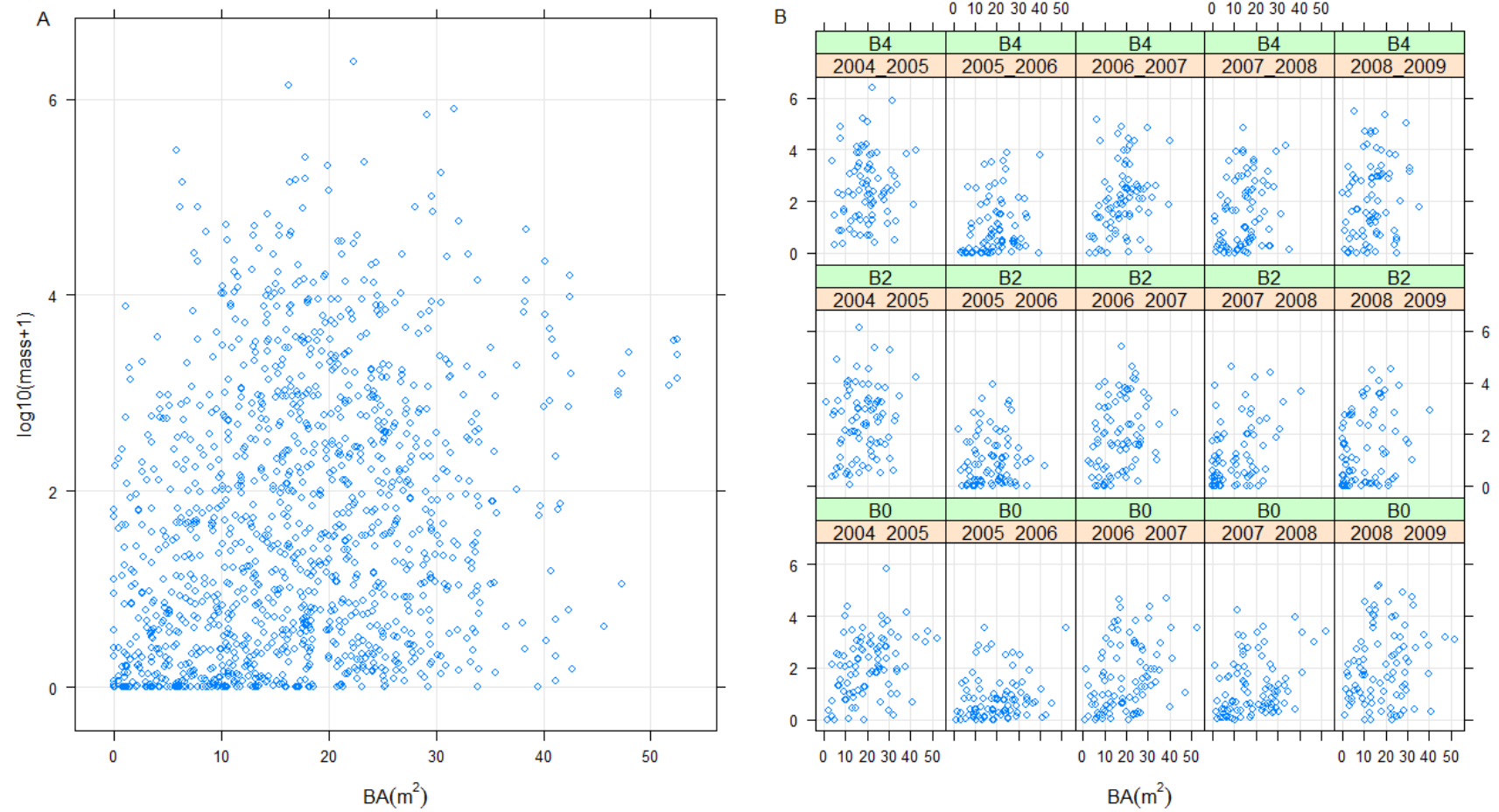


Figure A-2. Distribution of fruit-fall mass ($\log_{10}(\text{mass}+1)$) by live basal area (m^2) in trap centered plots. A) All treatments and years pooled ($R = 0.24$, $p < 0.001$; $\rho = 0.27$, $p < 0.001$). B) Grouped by treatment and year.

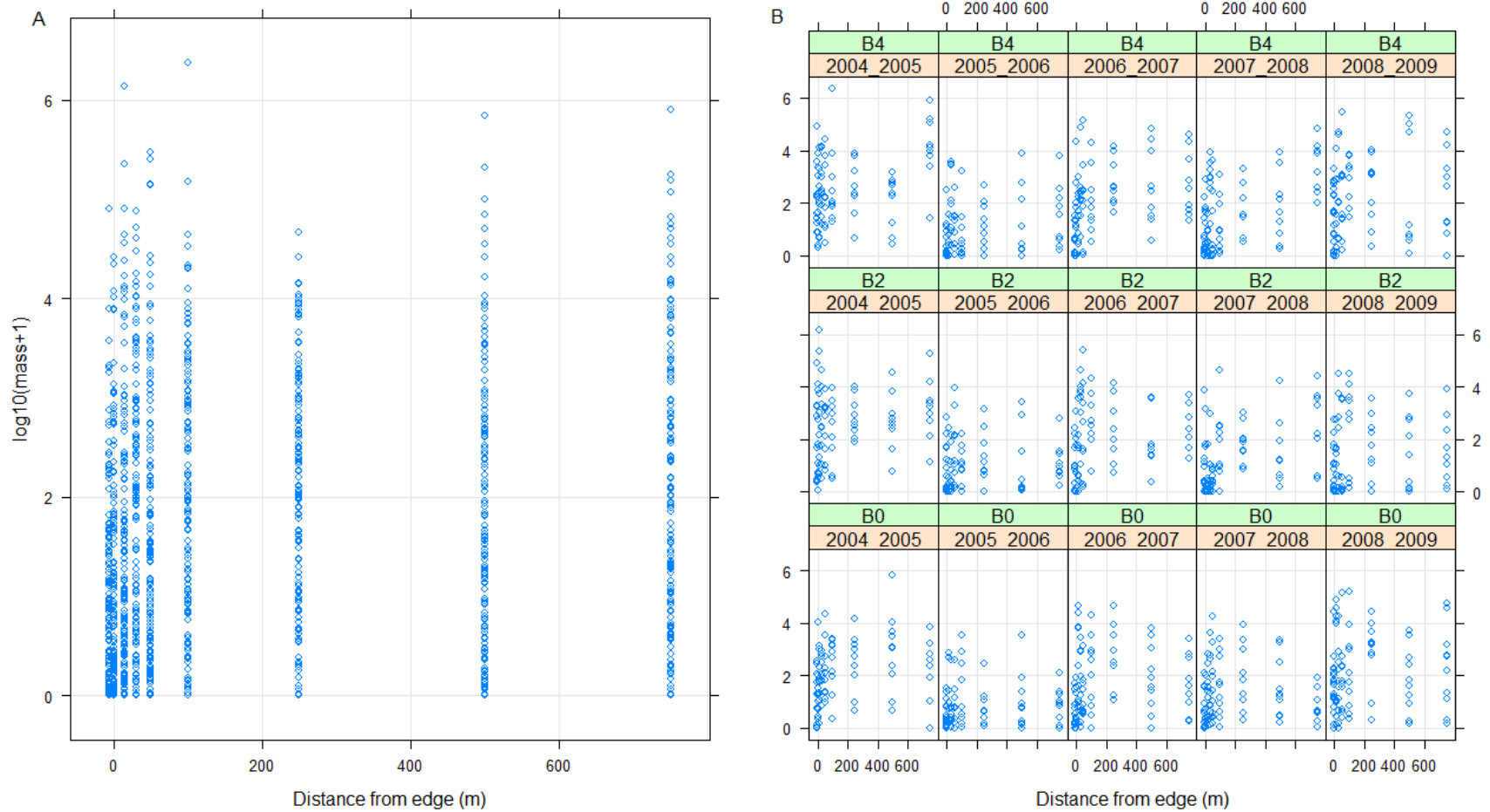


Figure A-3. Distribution of log-transformed fruit-fall mass ($\log_{10}(\text{weight}+1)$) by distance from the edge (m). A) All years and treatments pooled ($R = 0.19$, $p < 0.001$; $\rho = 0.29$, $p < 0.001$). B) Grouped by treatment and year.

Table A-1. Correlation between fruit-fall and tree and liana density by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.26*	0.28**	0.18	0.2	0.23*	0.23*	0.27*	0.28**	0.20	0.2
B2	0.20	0.18	0.07	0.13	0.29**	0.3**	0.55**	0.52**	0.39**	0.44**
B4	0.23*	0.25*	0.35**	0.39**	0.38**	0.42**	0.36**	0.38**	0.28*	0.31**

Table A-2. Correlation between fruit-fall and tree and liana basal area (m²) by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.34**	0.32**	0.18	0.21	0.36**	0.4**	0.28**	0.28**	0.19	0.2
B2	0.15	0.12	0.06	0.12	0.29**	0.31**	0.45*	0.44**	0.33**	0.37**
B4	0.11	0.07	0.24*	0.33**	0.33**	0.39**	0.26*	0.28**	0.22*	0.26*

Table A-3. Correlation between fruit-fall and distance from forest-agriculture edge (m) by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.27**	0.43**	0.07	0.18	0.14	0.32**	0.01	0.23*	0.1	0.19
B2	0.22*	0.26*	0.1	0.25*	0.15	0.32**	0.44*	0.49**	0.12	0.26**
B4	0.33**	0.29**	0.23*	0.37**	0.34**	0.47**	0.48**	0.44**	0.12	0.23*

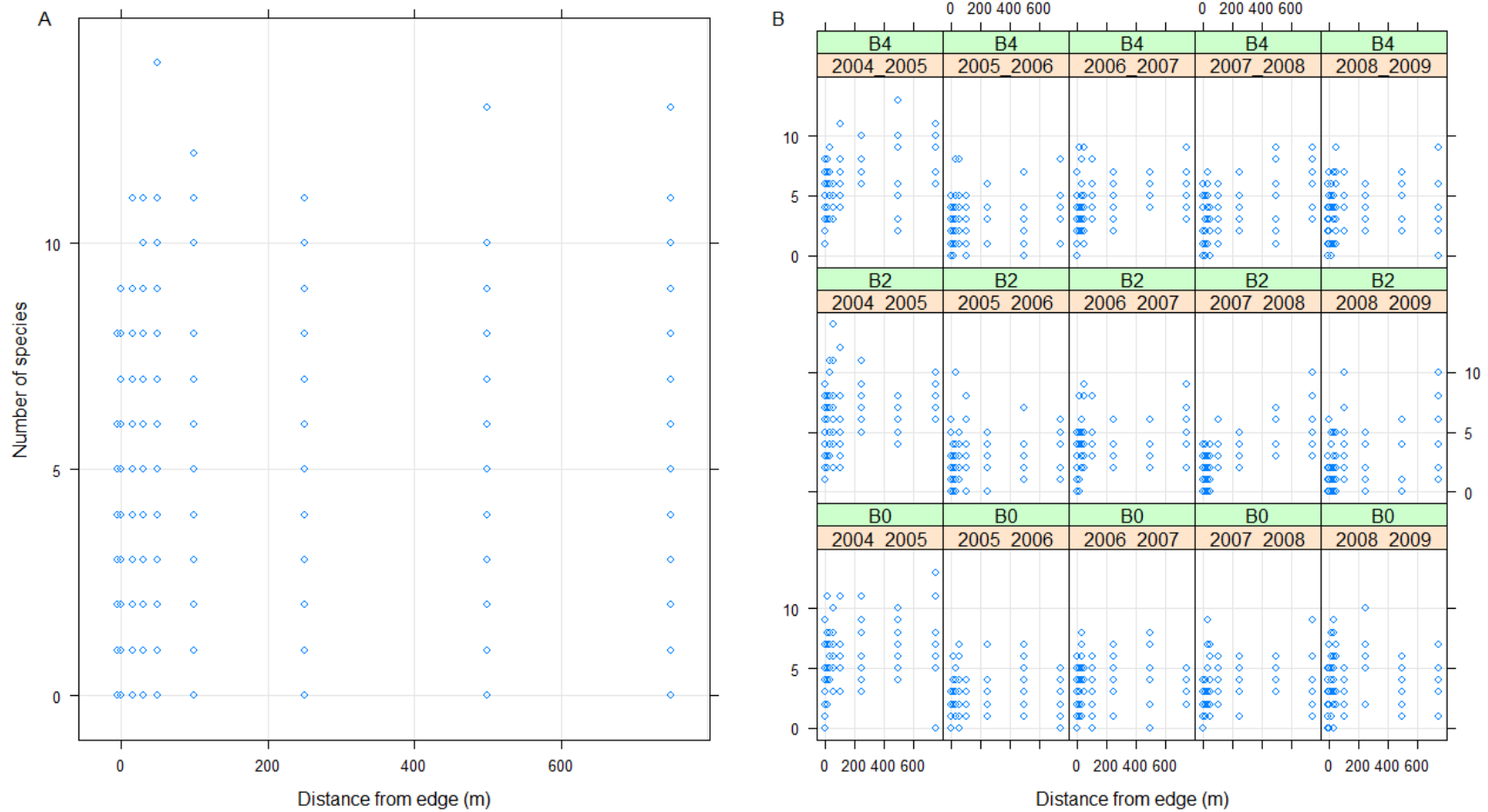


Figure A-4. Distribution number of species per trap and tree and distance from edge. A) All treatments and years pooled ($R = 0.25$, $p < 0.01$; $\rho = 0.34$ $p < 0.01$). B) Grouped by treatment and year.

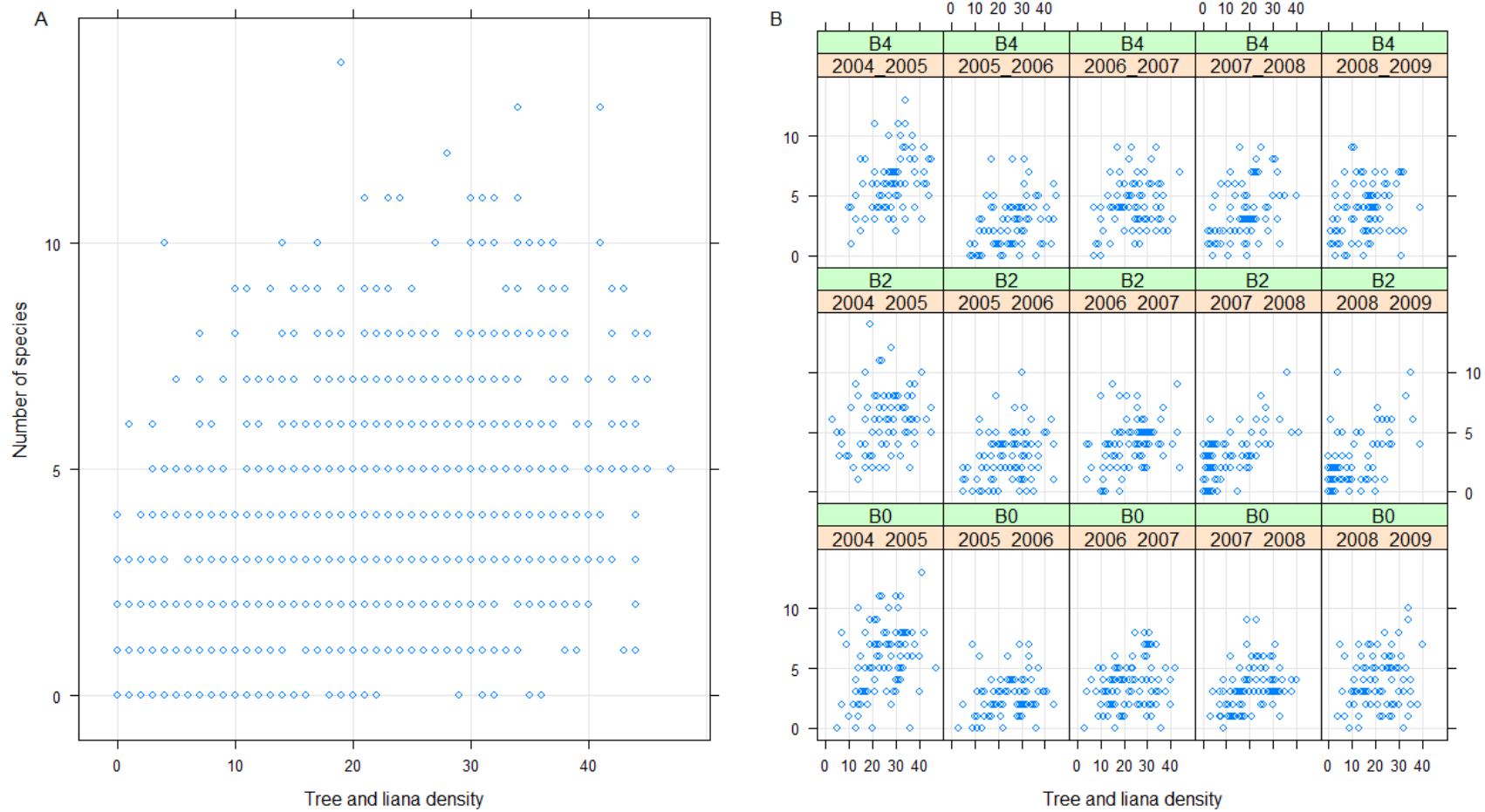


Figure A-5. Distribution number of species per trap and tree and liana density in trap centered plots. A) All treatments and years pooled ($R = 0.38$, $p < 0.01$; $\rho = 0.39$ $p < 0.01$). B) Grouped by treatment and year.

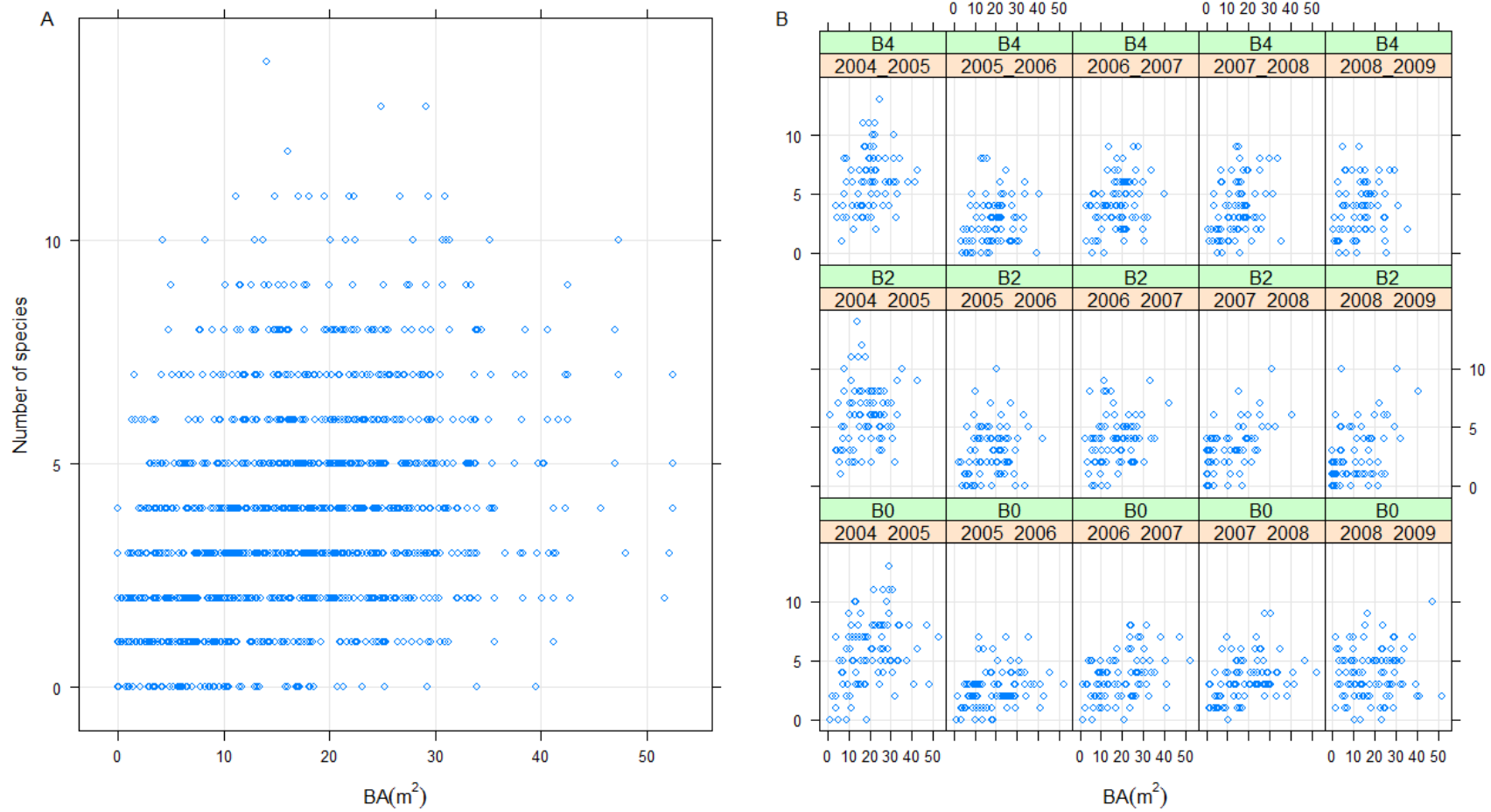


Figure A-6. Distribution number of species per trap and tree and liana basal area in trap centered plots. A) All treatments and years pooled ($R = 0.31$, $p < 0.01$; $\rho = 0.33$ $p < 0.01$). B) Grouped by treatment and year.

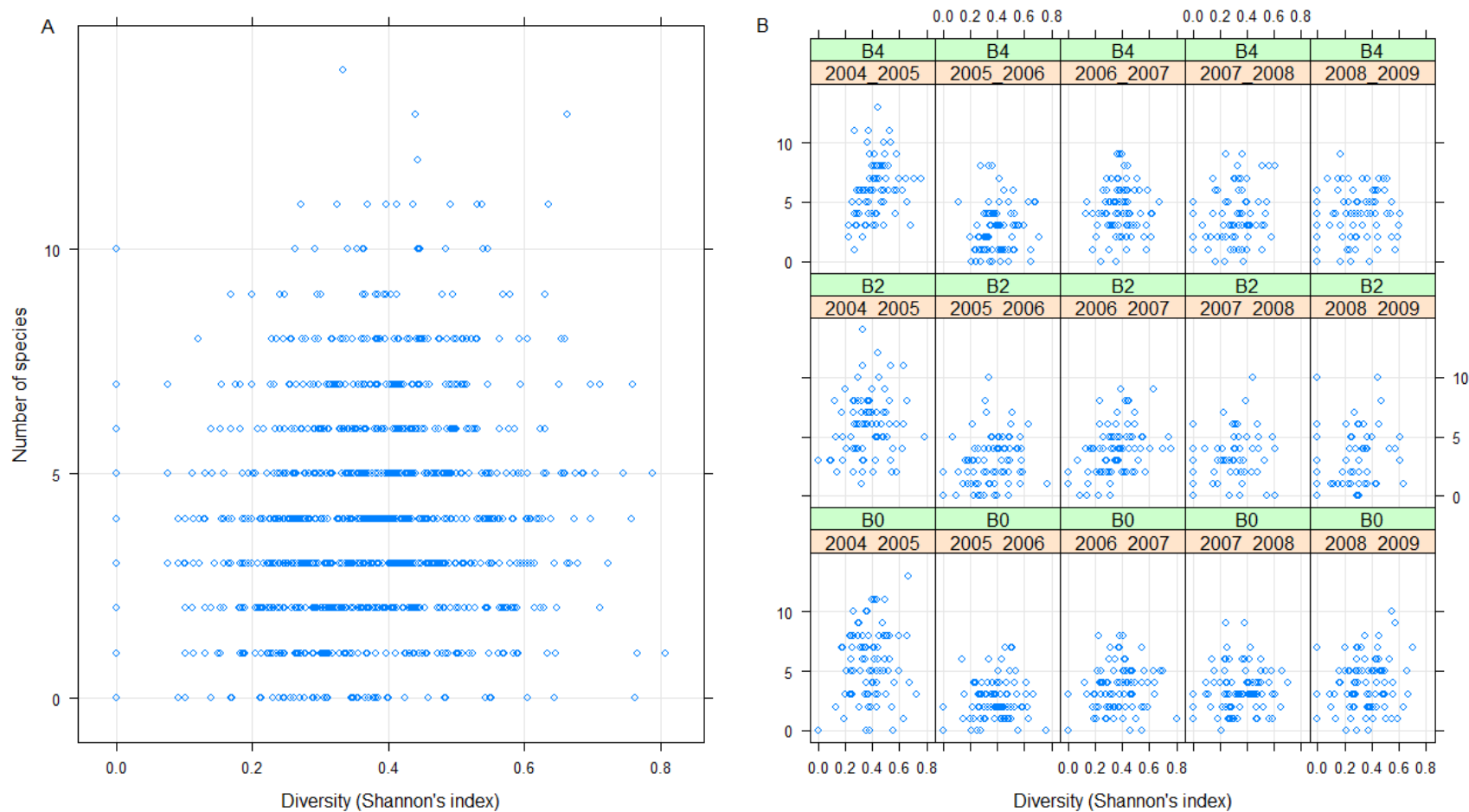


Figure A-7. Distribution number of species per trap and tree and liana diversity (Shannon's index) in trap centered plots. A) All treatments and years pooled ($R = 0.26$, $p < 0.01$; $\rho = 0.26$ $p < 0.01$). B) Grouped by treatment and year.

Table A-4. Correlation between fruit-fall species richness and distance from forest edge by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.34**	0.48**	0.12	0.24*	0.08	0.24*	0.29**	0.5**	-0.005	0.04
B2	0.23*	0.35**	0.3**	0.43**	0.24*	0.36**	0.66**	0.68**	0.4**	0.4**
B4	0.36**	0.43**	0.26*	0.34**	0.39**	0.48**	0.55**	0.52**	0.09	0.24*

Table A-5. Correlation between fruit-fall species richness and tree and liana density by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.38**	0.38**	0.26*	0.3*	0.22*	0.18	0.33**	0.4**	0.18	0.14
B2	0.25*	0.28*	0.27*	0.27*	0.35**	0.38**	0.65**	0.61**	0.58**	0.55**
B4	0.45**	0.48**	0.32**	0.36**	0.23*	0.16	0.43**	0.45**	0.24*	0.26*

Table A-6. Correlation between fruit-fall species richness and tree and liana basal area by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.35**	0.39**	0.27*	0.32**	0.36**	0.33**	0.35**	0.41**	0.07	0.05
B2	0.19	0.2	0.19	0.2	0.28*	0.3**	0.56**	0.54**	0.48**	0.45**
B4	0.29**	0.34**	0.21	0.27*	0.26*	0.24*	0.34**	0.37**	0.19	0.25*

Table A-7. Correlation between fruit-fall species richness and tree and liana diversity by year and treatment (r=Pearson's correlation, rho= Spearman's rank sum correlation, * = p<0.05, ** = p<0.01).

Year	2004-2005		2005-2006		2006-2007		2007-2008		2008-2009	
Treatment	r	rho	r	rho	r	rho	r	rho	r	rho
B0	0.1	0.05	0.07	0.06	0.09	0.12	0.1	0.1	0.15	0.13
B2	0.17	0.14	0.22	0.27*	0.39**	0.39**	0.36**	0.42**	0.39**	0.45**
B4	0.3**	0.39**	0.1	0.17	0.08	0.09	0.34**	0.34**	0.2	0.21

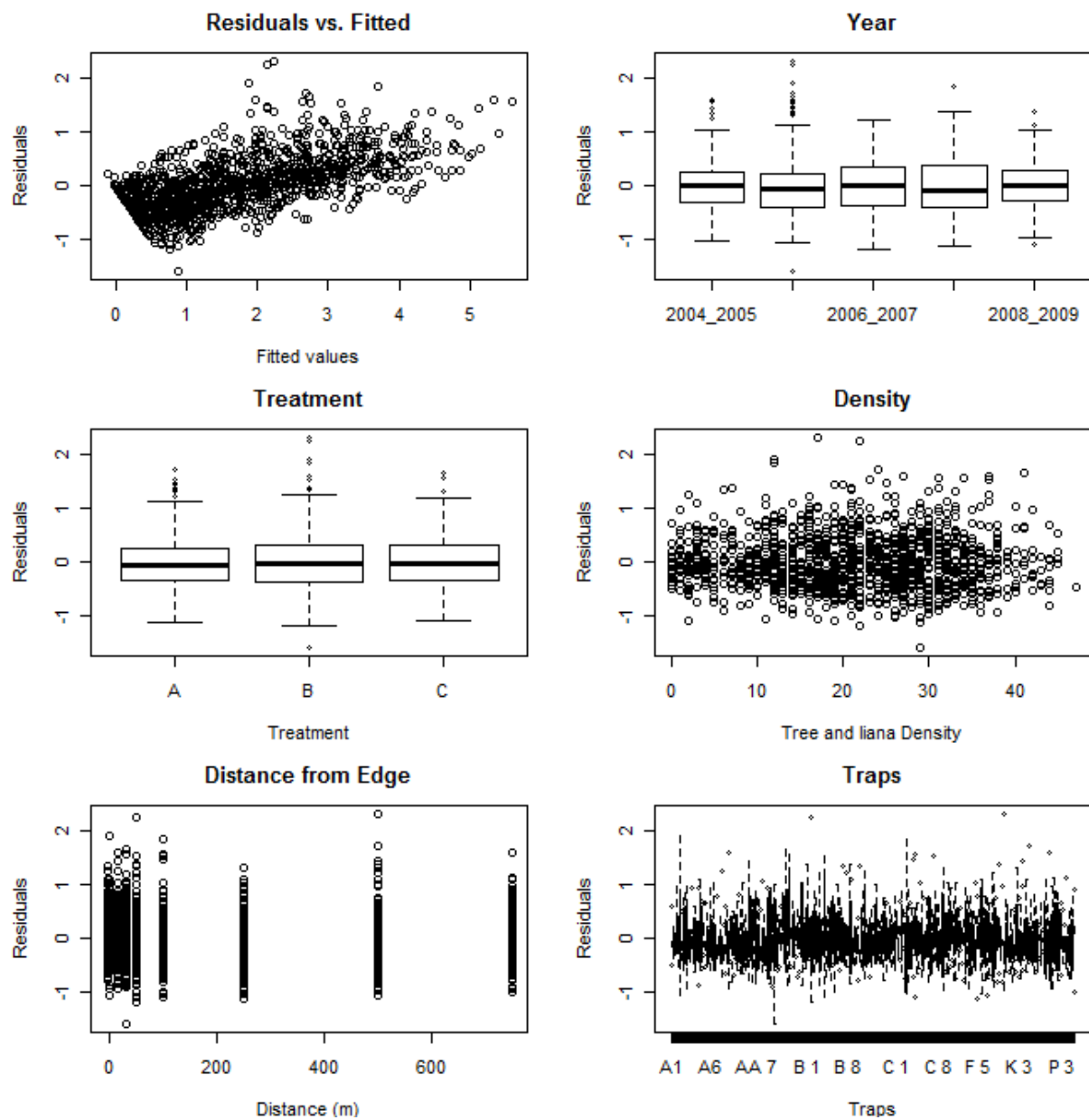


Figure A-8. Model residuals by fitted values and explanatory variables. Plot titles indicate variables used.

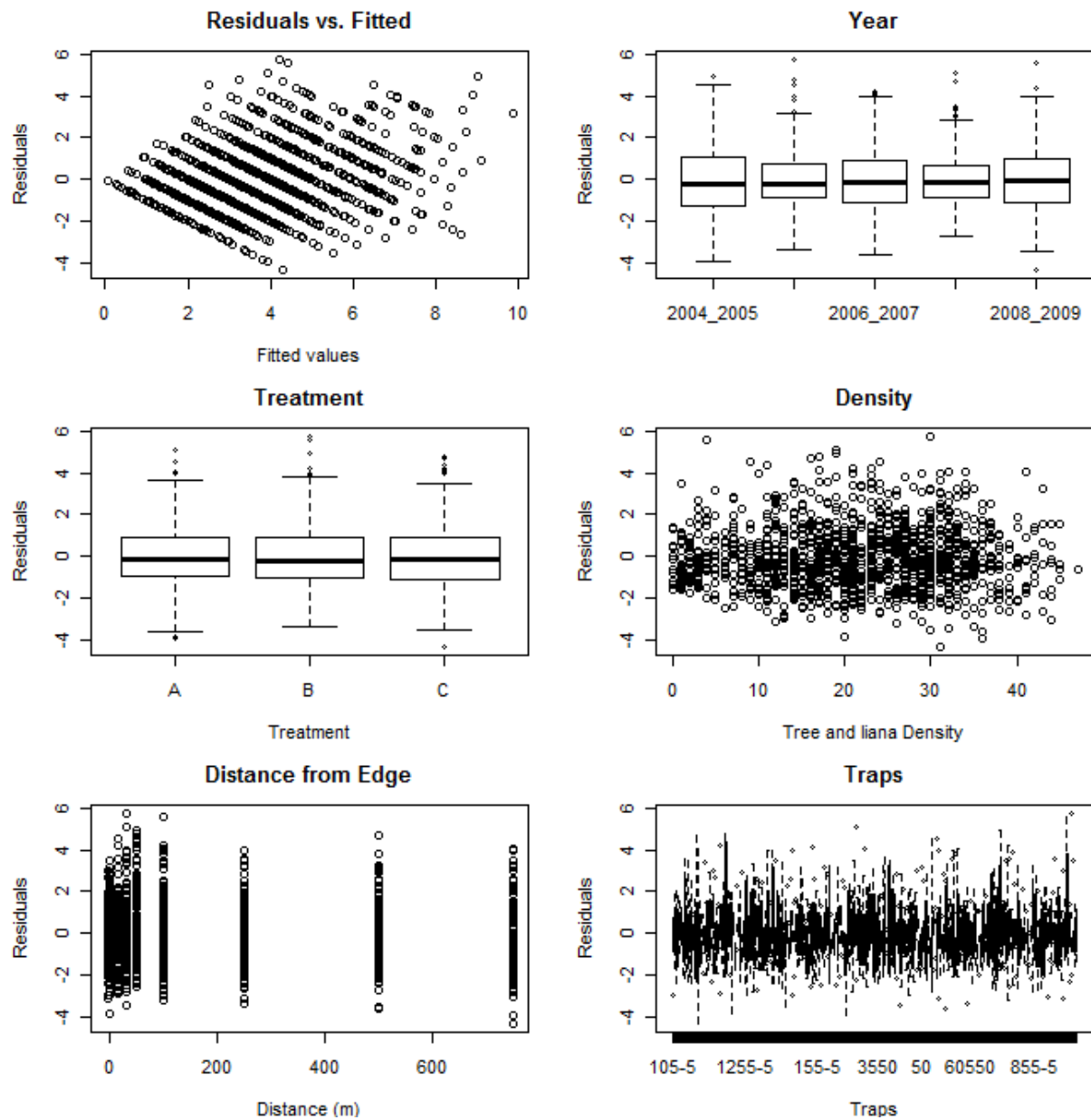


Figure A-9. Number of species model residuals by fitted values and explanatory variables. Plot titles indicate variables used.

LIST OF REFERENCES

- Balch, J. K., D. C. Nepstad, P. M. Brando, L. M. Curran, O. Portela, O. Carvalho, P. Lefebvre. 2008. *Global Change Biology* 14: 2276-2287.
- Balch, J. K., D. C. Nepstad, and L. M. Curran. 2009. Patterns and process: fire-initiated grass invasion at Amazon transitional forest edges. Pages 481 – 502 *in* M.A. Cochrane, editor. *Tropical fire ecology: climate change, land use, and ecosystem dynamics*. Springer, Berlin, Germany.
- Balch, J. K., D. C. Nepstad, L. M. Curran, P. M. Brando, O. Portela, P. Guilherme, J. C. Reuning-Scherer, and O. Carvalho. 2011. Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecology and Management* 261: 68-77.
- Barik, S. K., R. S. Tripathi, H. N. Pandey, and P. Rao. 1996. Tree Regeneration in a subtropical humid forest: effect of cultural disturbance on seed production, dispersal and germination. *Journal of Applied Ecology* 33: 1551-1560.
- Barlow, J. and C. A. Peres. 2004. Avifaunal responses to single and recurrent wildfires in Amazonian forests. *Ecological Applications* 14: 1358-1373.
- Barlow, J. and C. A. Peres. 2006a. Consequences of cryptic and recurrent fire disturbances for ecosystem structure and biodiversity in Amazonian forests. Pages 225 – 240 *in* W.F.Laurance and C.A. Peres, editors. *Emerging threats to tropical forests*. The University of Chicago Press, Chicago, Illinois, USA.
- Barlow, J. and C. A. Peres. 2006b. Effects of single and recurrent wildfires on fruit production and large vertebrates abundance in a central Amazonian forest. *Biodiversity and Conservation* 15: 985-1012.
- Barlow, J. and C. A. Peres. 2008. Fire-mediated dieback and compositional cascade in a Amazonian forest. *Philosophical Transactions of the Royal Society B* 363: 1787-1794.
- Barlow, J., T. Hugaasen, and C. A. Peres. 2002. Effects of ground fires on understory bird assemblages in Amazonian forests. *Biological Conservation* 105: 157-169.
- Bates, D., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-37. <http://CRAN.R-project.org/package=lme4>.
- Bond, W. J. and B. W. van Wilgen. 1996. *Fire and plants*. Chapman and Hall, London, UK.
- Chapman, C. A., R. Wrangham, and L. J. Chapman. 1994. Indices of habitat-wide fruit abundance in tropical forest. *Biotropica* 26: 160-171.

- Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51-71.
- Cochrane, M. A., A. Alencar, M. D. Schulze, C. M. Souza, D. C. Nepstad, P. Lefebvre, E. A. Davidson. 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests. *Science* 284: 1832-1835.
- Cochrane, M. A. 2003. Fire science for rainforests. *Nature* 421: 913-919
- Ghazoul, J., K. A. Liston, and T. J. B. Boyle. 1998. Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *Journal of Ecology* 86: 462-473.
- Godoy, J. A. and P. Jordano. 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology* 10: 2275-2283.
- Greene, D. F., C. Messier, H. Asselin, and M. Fortin. 2002. The effect of light availability and basal area on cone production in *Abies balsamea* and *Picea glauca*. *Canadian Journal of Botany* 80: 370-377.
- Guariguata, M. R. and G. P. Saenz. 2002. Post-logging acorn production and oak regeneration in a tropical montane forest, Costa Rica. *Forest Ecology and Management* 167: 285-293.
- Hoffmann, W. A. 1998. Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* 35: 422-433.
- Hojsgaard, S., U. Halekoh, J. Robinson-Cox, K. Wright, and A. A. Leidi. 2010. doBy: Groupwise summary statistics, general linear contrasts, LSMEANS (least-squares-means), and other utilities. R package version 4.1.2. URL <http://CRAN.R-project.org/package=doBy>.
- Holdsworth, A. R. and C. Uhl. 1997. Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecological Applications* 7: 713-725.
- Hulbert, S. H. 1984 Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- Karlsson, C. 2000. Seed production of *Pinus sylvestris* after release cutting. *Canadian Journal of Forest Research* 30: 982-989.
- Kauffman, J. B. 1990. Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica* 23: 219-224.

- Kennard, D. K., K. Gould, F. E. Putz, T. S. Fredericksen, and F. Morales. 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management* 162: 197-208.
- Lambert, F. R. 1992. The consequences of selectively logging for Bornean lowland forest birds. *Philosophical Transactions of the Royal Society B* 335: 443-457.
- Laurance, W. F. 2006. Fragments and fire: alarming synergisms among forest disturbance, local climate change, and burning in the Amazon. Pages 87 – 103 *in* W. F. Laurance and C. A. Peres, editors. *Emerging threats to tropical forests*. The University of Chicago Press, Chicago, Illinois, USA.
- Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos* 94: 27-38.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2011. *vegan: Community ecology package*. R package version 1.17-6. URL <http://CRAN.R-project.org/package=vegan>.
- Norden, N., J. Chave, A. Caubere, P. Chatelet, N. Ferroni, P. Forget, and C. Thebaud. 2007. Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. *Journal of Ecology* 95: 507-516.
- Peres, C. A., and M. van Roosmalen. 2002. Primate frugivory in two species-rich neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Pages 407- 421 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. *Seed dispersal and frugivory: ecology, evolution, and conservation*. CABI publishing, New York, New York, USA.
- Pinheiro, J., D. Bates, S. Debroy, D. Sarkar, and the R Development Core Team. 2010. *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-97.
- R Development Core Team. 2010. *R: A language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Ray, D., D. Nepstad, and P. Moutinho. 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecological Applications* 15: 1664-1678.
- Sanford, R. L., J. Saldarriaga, K. Clark, C. Uhl, and R. Herrera. 1985. Amazon rainforest fires. *Science* 227: 53-55.
- Sarkar, D. 2008. *Lattice: Multivariate data visualization with R*. Springer, New York, USA.

- Thiollay, J. 1997. Disturbance, selective logging, and bird diversity: a neotropical forest study. *Biodiversity and Conservation* 6: 1155-1173.
- Uhl, C., K. Clark, H. Clark, and P. Murphy. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. *Journal of Ecology* 69: 631-649.
- Uhl, C. and J.B. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71: 437-449.
- Veldman, J. W., B. Mostacedo, M. Pena-Claros, and F. E. Putz. 2009. Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. *Forest Ecology and Management* 258: 1643-1649.
- Wenger, K. F. 1954. The stimulation of loblolly pine seed trees by preharvest release. : 115-118.
- Whelan, R. J. 1995. *The ecology of fire*. Cambridge University Press, Cambridge, UK.
- Wickham, H. 2009. *ggplot2: Elegant graphics for data analysis*. Springer, New York, USA.

BIOGRAPHICAL SKETCH

Eric Oliveira Carvalho was born in Athens, Ohio and was raised in Salvador, Bahia, Brazil. Early in life he experienced a diversity of tropical ecosystems ranging from the rain forests of the Atlantic coast to the dry lands to the north and interior of the state. His interest in science was influenced by the scientific endeavors of his father on the field of geology and meteorite science. In 2000 Eric ingressed in the Universidade Federal de Vicosa in Minas Gerais, Brazil, to pursue a degree in Forest Engineering remaining in that institution until 2004. While at UFV he was exposed to research through the program for scientific initiation of the CNPq; he investigated the insects visiting flowers of Bignoniaceae in a forest fragment. In 2003, Eric was accepted as an exchange student between the UFV and the University of Florida and in 2004 transferred to UFL School of Forest Resources and Conservation from which he graduated in 2006 with a major in Natural Resource Conservation and minor in Wildlife Ecology and Conservation. During his undergraduate studies Eric worked on projects in the Atlantic Forest of Northeastern Brazil, on bees and forest ecology. Upon graduation he accepted a position of Forester with the US Forest Service at the Hiawatha National Forest on Michigan's Upper Peninsula. In that position he was involved in various aspects of forest management including timber marking, inventory, and timber sale preparation. It was during that time that his interest in fire ecology and management increased by working in iconic fire-dependant ecosystems such as Jack pine forests, training in fire management activities, and also through discussions with the forest's firefighters. In 2008 Eric was accepted to UFL graduate school to pursue a master's degree in Forest Ecology and Management with a concentration in fire ecology.